

ANATOMY, BIOLOGY AND SYSTEMATICS OF *CAMPANILE SYMBOLICUM*
WITH REFERENCE TO ADAPTIVE RADIATION OF THE
CERITHIACEA (GASTROPODA: PROSOBRANCHIA)

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ABSTRACT

Campanile symbolicum Iredale is the sole survivor of a long lineage of large mesogastropods in the family Campanilidae. The family was well represented in the Tethys Sea and underwent a widespread adaptive radiation in the early Tertiary. Several of the fossil species are among the largest known gastropods. The living relict is confined to southwestern Australia where it is common in shallow, subtidal, sandy habitats. It is a herbivore with a generalized taenioglossate radula and thick jaws. The large, elongate conical shell has a chalky periostracum and the aperture, which has a central anterior canal, is at a 45 degree angle to the shell axis. The open pallial gonoducts in both sexes and aphyllid males are conservative characters found in all cerithiaceans. These, and the characters derived from the shell, operculum and radula unequivocally refer *Campanile* to the superfamily Cerithiacea. Anatomical features of the sensory, reproductive, alimentary and nervous systems of *Campanile* are unique among the Cerithiacea and indicate that it should be allocated to a separate family, the Campanilidae.

Among the external anatomical features peculiar to *Campanile* are a short thick snout, tiny eyes, and a deep ciliated pedal gland around the entire margin of the sole of the foot. Small papillae surround the entire mantle edge. The columellar muscle is long and has a large prominence. A short oval bipectinate osphradium is located at the anterior end of the mantle cavity adjacent to the long ctenidium. It closely resembles the osphradia of neogastropods and several families of higher mesogastropods. The hypobranchial gland is modified into tiny leaflets where it is adjacent to the anus. Two simple laminae comprise the pallial oviduct and are longitudinally folded. The internal folds of the proximal end of the left lamina of the pallial oviduct are elaborated into broadly ovate transverse ridges forming a large albumen gland. A sac-like seminal receptacle projected into the pericardial sac opens into the left proximal end of the pallial oviduct. It occurs in both sexes but is more highly developed in females. Although sexes are separate, this suggests that *Campanile* is a protandric hermaphrodite. The head and foot of a mature animal become bright pink. It appears that *Campanile* forms spermatophores. Sperm taken from the vas efferens are all eupyrene. Spawn masses are large gelatinous tubes deposited on the substratum and contain spirally arranged capsules, each of which contains one to several moderately sized eggs. Development is either direct or with a short demersal larval stage. Veliger stages are attained within the spawn mass and the embryonic shell is smooth, bulbous and lacks a sinusigera notch. The radula of *Campanile* is wide and robust but unusually short in comparison to the size of the snail. Paired salivary glands and their ducts and paired buccal pouches lie anterior to the nerve ring. The mid-esophagus encloses the dorsal and ventral food channels. It has shallow lateral folds but no esophageal gland and is surrounded by a large mass of connective tissue in the middle of which is a thin muscular sheet. The stomach has a style sac but lacks a gastric shield and a style. In the sorting area is a series of leaflets spirally arranged in a deep pit. In the posterior of the stomach is the vestige of a spiral caecum. The nervous system comprises a mixture of loosely connected and condensed ganglia and is dialyneurous and zygoneurous.

The Campanilidae appeared in the late Cretaceous to early Tertiary as did most other substantial cerithiacean families. Each family radiated into a specific adaptive niche and has remained essentially the same in ecology and general physiognomy of its members. Although the Campanilidae were abundant in the Paleocene and Eocene, it is the only cerithiacean family to have undergone serious diminution in species to the point of virtual extinction. Campanilid snails were the largest animals in the superfamily and were undoubtedly grazers of microalgae in the shallow waters of the Tethys. A hypothesis for the demise of the Campanilidae is trophic competition with another group of large grazing gastropods, the Strombidae, which became established in the late Eocene to early Miocene and flourished in a similar ecological niche.

INTRODUCTION

During the early Tertiary, genera of the family Campanilidae Douvillé, 1904, were a group of many species that were common in the Tethys Sea. There is an extensive literature about these spectacular gastropod fossils. Some species, such as *Campanile giganteum* (Lamarck, 1804), attained a length of 1 m and are among the largest gastropods on record. The family is represented today by a single living species: *Campanile symbolicum* Iredale, 1917, from southwestern Australia.

This living species is a subtidal, shallow-water dweller that is common within its limited range. Although it is unusually large for a cerithiid, and a relict species of an extinct group, it is not well known to malacologists and is poorly represented in museum collections outside Australia. Virtually nothing has been published about its ecology or life history and no recent comprehensive account of the anatomy of this interesting animal exists; consequently, its relationship to other cerithiacean groups and to the numerous fossil species within the family Campanilidae is conjectural and is based solely on shell characters. Indeed, some authors have questioned whether *Campanile symbolicum* is of the same lineage as the larger Tethyan fossils.

Much of the literature on this group has dealt with the selection of a proper type-species for the genus and with nomenclatural problems. The nomenclature of the generic and specific names has a complex history.

In May, 1979, I observed a population of *Campanile symbolicum* at Pt. Peron, near Perth, Western Australia. I studied the living animals and dissected narcotized specimens in order to make anatomical comparisons with other cerithiaceans. Egg masses and embryos were also studied.

This paper presents my findings and includes an historical review of the genus *Campanile*. My description of *Campanile symbolicum* includes anatomical, embryological, opercular and radular characters as well as shell features. I also include some aspects of the reproductive biology and brief notes on the ecology of the species. These findings indicate that *Campanile* should be assigned to a separate family, Campanilidae. The relationship of this relict family to other families within the Cerithiacea reflects the adaptive radiation of the superfamily.

MATERIALS AND METHODS

Specimens were collected by hand while snorkeling from Pt. Peron, Western Australia and living animals were examined in the field to determine their exact habitat. Individual snails were maintained in seawater aquaria at the Western Australian Museum, Perth, for behavioral observations. For anatomical studies, animals were extracted from their shells that had been cracked with a large vise and were relaxed in 7.5% MgCl₂. Dissections were made with the aid of a binocular dissecting microscope. Material for histological sections was prepared in Bouin's Fixative, embedded in paraffin and sectioned on the microtome at 5 μm. Sections were stained with Harris' hematoxylin and counterstained with Eosin Y. The radula, jaws, periostracum and shell ultrastructure were studied with a scanning electron microscope. The geographic range of the species was determined by examination of specimens in major museums in the United States and Australia, and statistics of shell measurements computed from a large series of adult shells. Preserved spawn masses and embryos were studied with a Wild stereo dissection scope and a scanning electron microscope was used to study embryonic shells.

KEY TO ABBREVIATIONS ON FIGURES

a	—anus
aa	—anterior aorta
ag	—albumen gland
as	—attachment surface
au	—auricle
b	—baffle
bg	—buccal ganglion
bm	—buccal mass
bp	—buccal pouch
bv	—blood vessel
cem	—cut edge of mantle
cf	—ciliated furrow
cm	—columellar muscle
cnt	—connective tissue
ct	—ctenidium
ctb	—ciliated tube
ctr	—ciliated tract
dg	—digestive gland
dol	—division of outer lamina
dpg	—distal part of pallial oviduct
dsr	—duct of seminal receptacle

- ebv —efferent branchial vessel
 es —esophagus
 eso —esophagus opening
 ev —esophageal valve
 exs —exhalant siphon
 f —foot
 ff —fold emerging from spiral caecum
 fg —food groove
 FL —sperm flagellae
 gil —glandular part of inner lamina
 gs —“gastric shield”
 gsa —grooved channel
 H —head of sperm
 hg —hypobranchial gland
 il —inner lamina
 ins —inhalant siphon
 int —opening to intestine
 j —jaw
 k —kidney
 ko —kidney opening
 lcg —left cerebral ganglion
 ld —lower duct
 les —lumen of esophagus
 lhg —leaflets of hypobranchial gland
 lpg —left pleural ganglion
 lpn —left pallial nerve
 mc —mantle cavity
 me —mid-esophagus
 ml —thin muscular layer
 mp —mantle papillae
 od —odontophore
 odg —oviducal groove
 odu —oviduct
 OES —opening to esophagus
 ol —outer lamina
 op —operculum
 opn —optic nerve
 os —osphradium
 osr —opening of seminal receptacle
 ov —ovary
 pp —propodium
 ppg —proximal part of pallial oviduct
 ps —pericardial sac
 r —rectum
 ra —radula
 rcg —right cerebral ganglion
 rl —renal lamellae as seen by transparency
 rpd —renopericardial duct
 rpg —right pleural ganglion
 RW —receptacle wall
 sa —sorting area
 sc —spiral caecum
 sec —supraesophageal connective
 seg —supraesophageal ganglion
 sg —salivary gland
 sl —sorting leaflets
 sn —snout
 sp —sperm in smooth chamber
 sr —seminal receptacle
 ss —style sac
 st —stomach
 t₁ —major typhlosole
 t₂ —minor typhlosole
 tn —tentacle nerve
 ve —ventricle
 wps —wall of pericardial sac
 z —zygoneury between right pleural ganglion and subesophageal ganglion.

DESCRIPTION

This section deals with the descriptions of the shell, operculum, radula, anatomy, spawn and larvae of *Campanile symbolicum*, and will bring together my own observations and those of previous authors. The anatomical description includes external and internal features and is supplemented with histological studies. The functional interpretations of various systems are proposed and most of the significant anatomical features are figured. Brief discussions on ecology and the fossil history of *Campanile* are included.

Specimens examined—Great Australian Bight (NMV); Recherche Archipelago, 23°15'S, 122°50'E, including Mondrain Id., Salisbury Id., Middle Id., Boxer Id. (all NMV); Nares Id., Duke of Orleans Bay (WAM); Lucky Bay (WAM); Two Mile, Hopetoun (AMS, WAM); Bremer Bay (WAM); Princess Royal Harbour (AMS); Pallinup River Estuary (WAM); Point Irwin (DMNH); South Point, S side of Two People Bay, Albany (AMS); Irwin River Inlet, W of Albany (AMS); Middletown Beach, Albany (WAM); Frenchman's Bay, Albany (WAM); Albany (ANMH); Cowaramup Bay (AMNH); Augusta (WAM); Sarge Bay; Cape Leeuwin (WAM); Hamelin Bay (WAM); Bunker Bay, Cape Naturaliste (WAM, USNM, ANSP, MCZ); N side of Cape Naturaliste Light (AMS, USNM); Busselton (WAM); Dunsborough (WAM, AMNH); Yallingup Brook (WAM, NMV); Yallingup (WAM, NMV, AMS); Canal Rocks, S of Yallingup (AMS); Geographe Bay (AMS); Cape Mentelle, Kilcarneys (AMS); Bunbury, reef at Capel (AMS); W side of Carnac Id. (WAM); Rockingham (AMS); Fremantle (ANSP, DMNH, WAM); near Garden Id., Fremantle (MCZ);

SW of Garden Id., Fremantle (AMS); Kwinana (AMS); Dunn Bay (USNM); Swan River (NMV); Cottesloe (WAM); Carnac Id. (WAM); Point Peron, Perth (AMNH, WAM, USNM); Trigg Id. (WAM); Yanchep Reef (WAM); Pal-linup Estuary (WAM); Port Denison (WAM); Jurien Bay (WAM); Dongara (AMS); Beach Colony Shore, Geraldton (MCZ, AMS).

Shell description (Figs. 1–2)—Shell large, ranging from 60 to 244 mm in length (See Table 1 for measurements), turreted, elongate, having apical angle of 25° and teleoconch of about 25–30 flat-sided whorls that become weakly inflated or angular on penultimate and body whorls. Outline of entire spire concave and early whorls usually missing. Each whorl

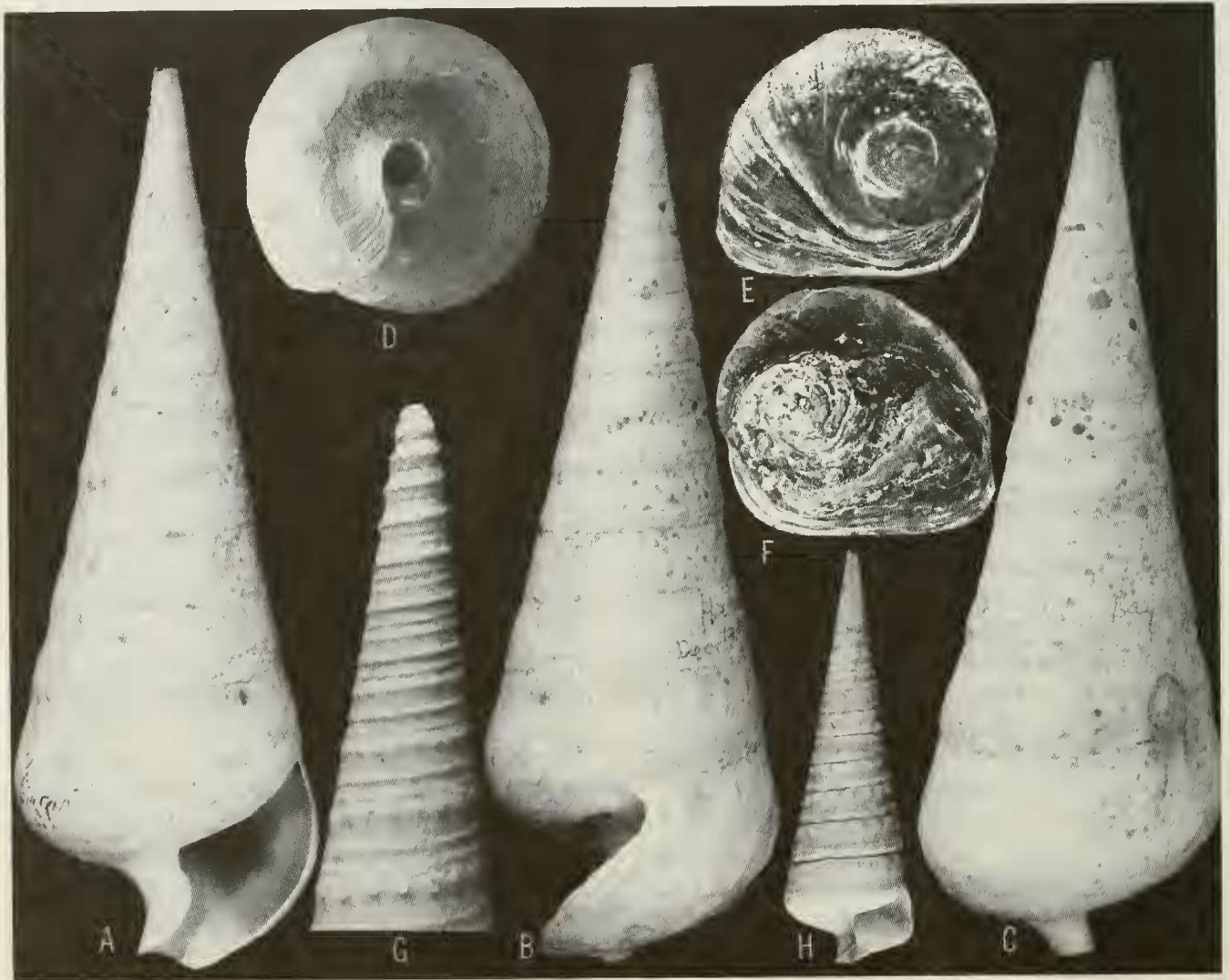


FIG. 1. A–F, Shell and operculum of *Campanile symbolicum* from Hamelin Bay, Western Australia (Western Australian Museum N4514), 120 mm long, 68 mm wide; operculum 17 mm diameter. A, Apertural view; B, Side view showing sinuous outer lip; C, dorsal view; D, Anterior view of centrally placed siphonal canal; E, Free surface of operculum showing subcentral nucleus; F, Attachment surface showing large oval muscle scar on lower two thirds of operculum; G, Detail of sculpture of early whorls on specimen from Salisbury Id., Recherche Archipelago, Western Australia (National Museum, Victoria); H, Holotype of *Cerithium leve* Quoy & Gaimard (National Museum of Natural History, Paris, photograph courtesy of Mr. Foubert).

FIG. 2. *Campanile symbolicum*. a–c, Advanced embryonic shells from egg mass found at Rottnest Id., Western Australia (diameter, 0.05 mm); d, SEM of single jaw showing attachment surface (5 mm long); e, SEM of jaw showing cutting edge (5 mm long); f, Longitudinally cut shell showing apex with calcareous septa in interior whorls; g, Whole shell cut longitudinally from apex to anterior canal showing whorl configuration and columella; h, SEM of cross section of jaw, showing four layers, about .055 mm wide. The bottom layer is the attached portion; i, SEM enlargement of attachment surface of jaw showing microscopic polygonal pits, each about $7 \mu\text{m}$ long; j, SEM detail of surface periostracum showing cancellate, pitted appearance, $28\times$; k, SEM detail of cross section of shell showing, from top to bottom, calcified periostracum with subsurface tubules, and cross lamellar aragonite, $86\times$.

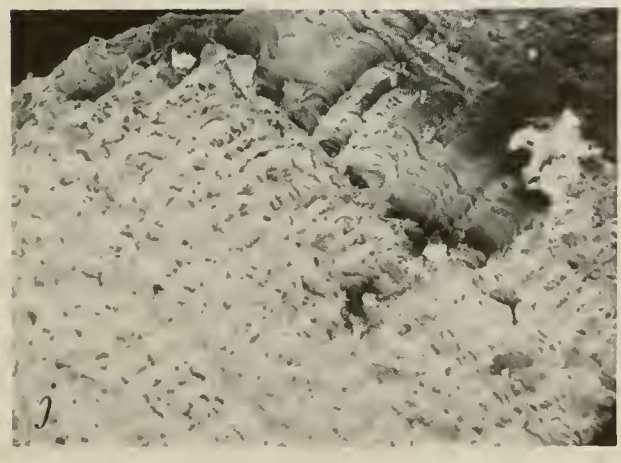
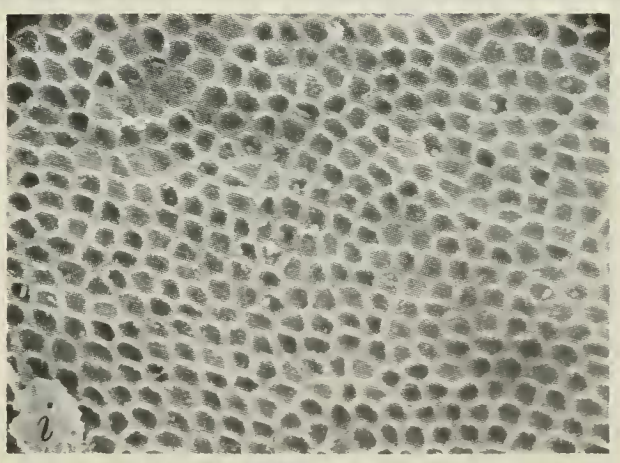
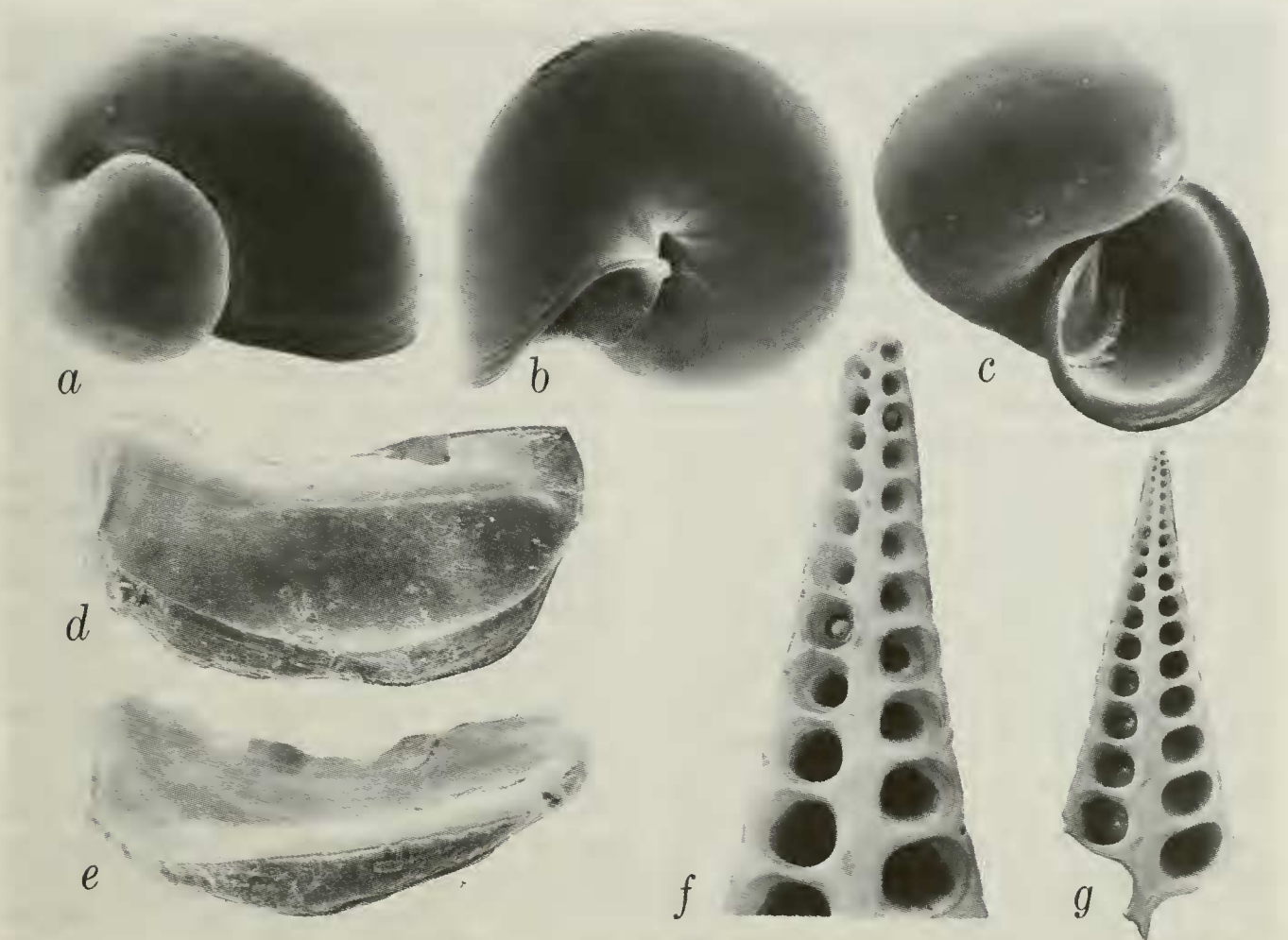


TABLE 1. Statistical summary of shell measurements of *Campanile symbolicum* (in mm).

Character	Number	Range	Mean	SD
Length	29	60–244	142.8	50.84
Width	29	21.5–74	44.1	15.81

sculptured with a presutural spiral cord that produces a weak keel at the base. This spiral cord is more medianly placed on very early whorls and may be divided into two spiral cords on some shells. Early whorls and mid whorls have a subsutural spiral that tends to disappear on later whorls (Fig. 1G). Nodules frequently elongated axially, sometimes entirely absent. Penultimate and body whorls usually smooth. Below nodules each whorl sculptured with many microscopic spirally incised lines that are crossed over by numerous axial, sinuous, growth lines. Suture distinct and straight. Protoconch (Fig. 2a–c) smooth, bulbous, about 1½ whorls. Protoconch lip slightly flared at base. Body whorl is round with the anterior siphonal canal in the center. Aperture triangular-fusiform and at a 45° angle to axis of shell. Aperture one-fourth to one-fifth the length of shell. Interior of aperture glossy white. Anterior siphonal canal distinct, deep and moderately short, almost straight but slightly twisted to left of shell axis. Columella short, concave and twisted slightly to left at anterior canal. A slight plait appears at the columella base but does not continue into the aperture and up the axis of the shell. Older, larger specimens have an inner columellar lip, slightly detached from parietal area. Outer lip thin, sinuous, smooth and with a deep sinus where attached to body whorl. Lower portion of outer lip crosses over anterior canal when shell is viewed anteriorly.

A shell cut in half longitudinally, from apex to anterior canal, exposing the whorl interiors reveals that the columella is concave throughout the shell axis and that each whorl is round in cross section (Fig. 2f,g). Scanning electron micrographs of cross section of the shell wall show that it is composed of cross lamellar aragonite which appears in a wide bottom layer overlain with looser disordered aragonite (Fig. 2k).

The periostracum of *Campanile* is unusual and closely resembles that of some muricid gastropods such as those in the genus *Aspella* Mörch. It is thick and comprises a cancellate, calcified outer layer and an under-

lying scabrous layer (Fig. 2i,j). Radwin & D'Attilio (1976: 245) considered this to be a chalky white surface layer of the shell and called it the "intritacalx" but it is simply the calcified outer portion of the periostracum (Waller, personal communication), as can be seen in scanning electron micrographs of the fractured shell edge (Fig. 2k). In *Campanile*, the outer calcified layer of the periostracum has a cancellate appearance at the surface that is most clearly seen in young specimens. Beneath the surface are numerous fine hollow tubes that run spirally around each whorl. This layer is fragile and flakes off easily in dried specimens. In older shells the surface appears to be pitted and chalky. The pits are merely depressions formed by the cancellate pattern in the outer layer. Wrigley (1940: 99) noted tiny pitted lines on the surface of all fossil species of *Campanile* he examined and I have also seen this pattern on fossils of *Campanile giganteum*. This calcified thick periostracum thus appears to be a characteristic of the family Campanilidae.

The brown-colored operculum (Fig. 1E–F) is corneous, moderately thick and paucispiral with a subcentral nucleus. The operculum has a straight growing edge and the edge nearest the nucleus is partially covered with the foot when the animal is extended. The ovoid attachment scar is on the obverse, bottom two-thirds of the operculum (Fig. 1F). The operculum diameter is much smaller than that of the aperture, allowing the animal to retract deeply into the mid whorls of the shell. In this retracted state, the operculum fits snugly into the shell aperture.

Animal (Figs. 3–7)—A brief but accurate description of the animal was given by Quoy & Gaimard (1834: 107–108) in the original description. A more detailed account of the gross anatomy that centered on the nervous system but included observations of other systems was presented by Bouvier (1887a,b), who compared *Campanile* with other cerithiids. Although Bouvier's (1887b) work is accurate and thorough, he failed to describe the reproductive tract which is essential for an analysis of comparative relationships among cerithiaceans. Bouvier's papers were published in French journals that were apparently missed by subsequent authors.

The only figure of a living animal of *Campanile* is the one originally given by Quoy & Gaimard (1833: pl. 54, fig. 2), and it only shows the head-foot. Part of the foot covers the edge of the operculum nearest the oper-

cular nucleus. If the shell is cracked, the snail may withdraw as far as one-half the length of the shell, causing the edges of the operculum to fold.

When animals are extracted from their shells it is apparent that the upper portion of the visceral mass, comprising the digestive gland and gonad, does not fill the upper whorls of the shell apex. These are walled off by a series of concave, calcareous partitions or septa and the earliest whorls are totally

filled. The concavity of each septum is adapical (Fig. 2f-g). Just anterior to the last septum the shell whorls are lined with a thin brown membrane. Attached to this membrane is another thin, transparent, membrane that is invested with tiny brown spherules of unknown function. Both of these membranes are of obvious organic origin and are probably laid down by the mantle.

The head-foot and mantle edge of live snails from Point Peron are white to flesh

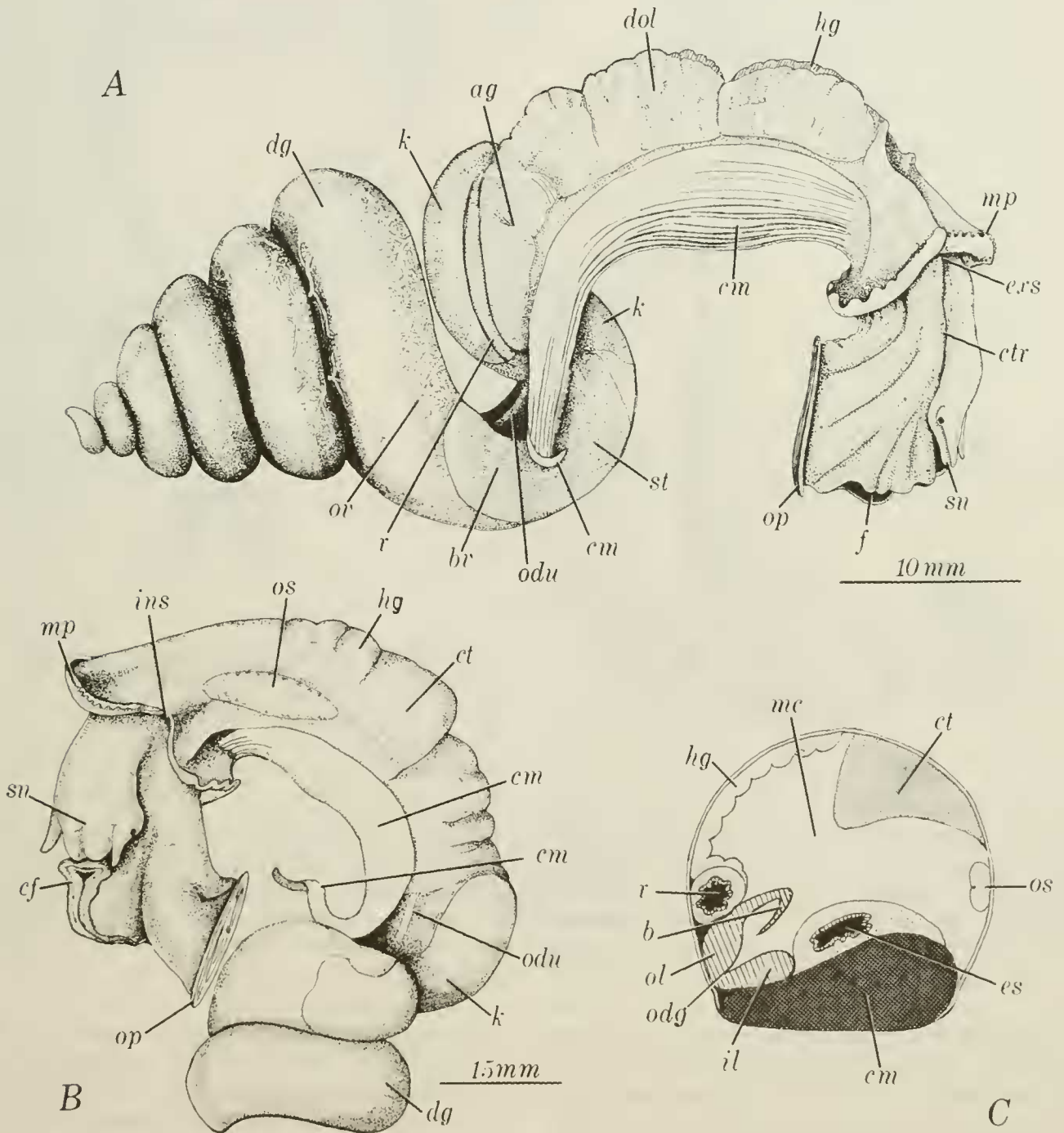


FIG. 3. *Campanile symbolicum*, removed from shell. A, View of right side of female showing major external structures and free part of columellar muscle; B, Left side of animal; C, Cross section of female through mid mantle cavity showing relationship of major pallial organs. (See Key to Abbreviations, p. 264, for explanation of lettering.)

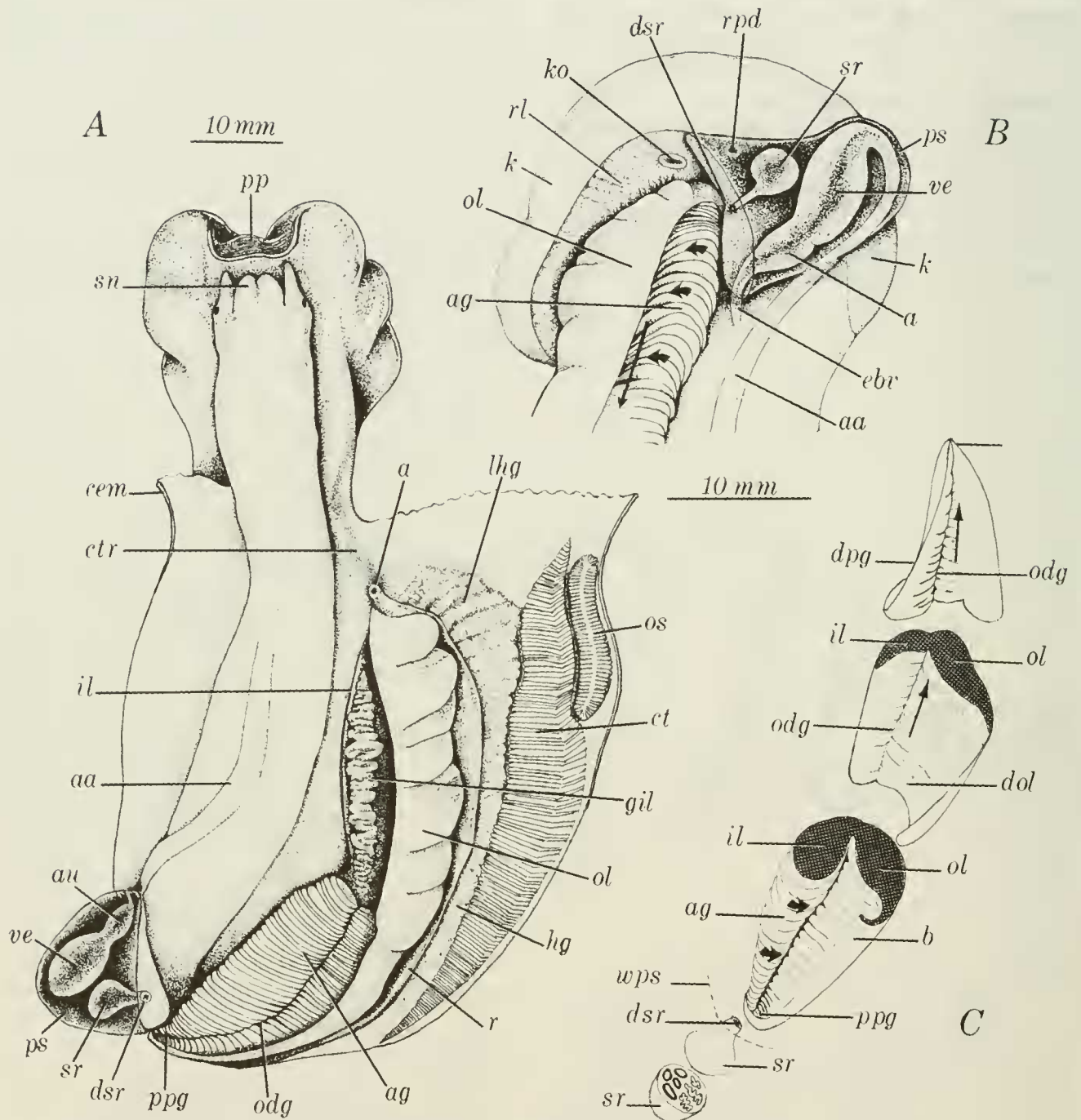


FIG. 4. Internal anatomy of *Campanile symbolicum*. A, Female removed from shell with mantle cavity opened with a lateral-dorsal cut; B, Detail of proximal portion of pallial oviduct showing relationship of kidney, pericardial sac and seminal receptacle to oviduct. The kidney has been pulled back to expose the proximal part of the pallial oviduct; C, Diagrammatic representation of sections of pallial oviduct and seminal receptacle showing major anatomical features. Compare with pallial oviduct depicted in drawing A, this figure. (See Key to Abbreviations, p. 264, for explanation of lettering.)

colored and slightly mottled with light brown and pink. Extracted snails are small in relation to their shells. The snout is short, broad and thick and is conspicuously bilobed at the tip (Fig. 3B, *sn*). Tentacles are short and bright pink, each with a tiny black eye at its broad base.

Emerging from the exhalant pallial siphon (Fig. 3A, *exs*) and running down the right side

of the head-foot, beneath the right eye and tentacle and down the outer surface of the foot is a deep ciliated groove (Figs. 3A, 4A, *ctr*) in which fecal pellets and other debris are expelled from the mantle cavity in a string of mucus. This is probably also used by females during oviposition. Although I found no evidence of a structure that could be interpreted as an ovipositor, one associated with this cili-

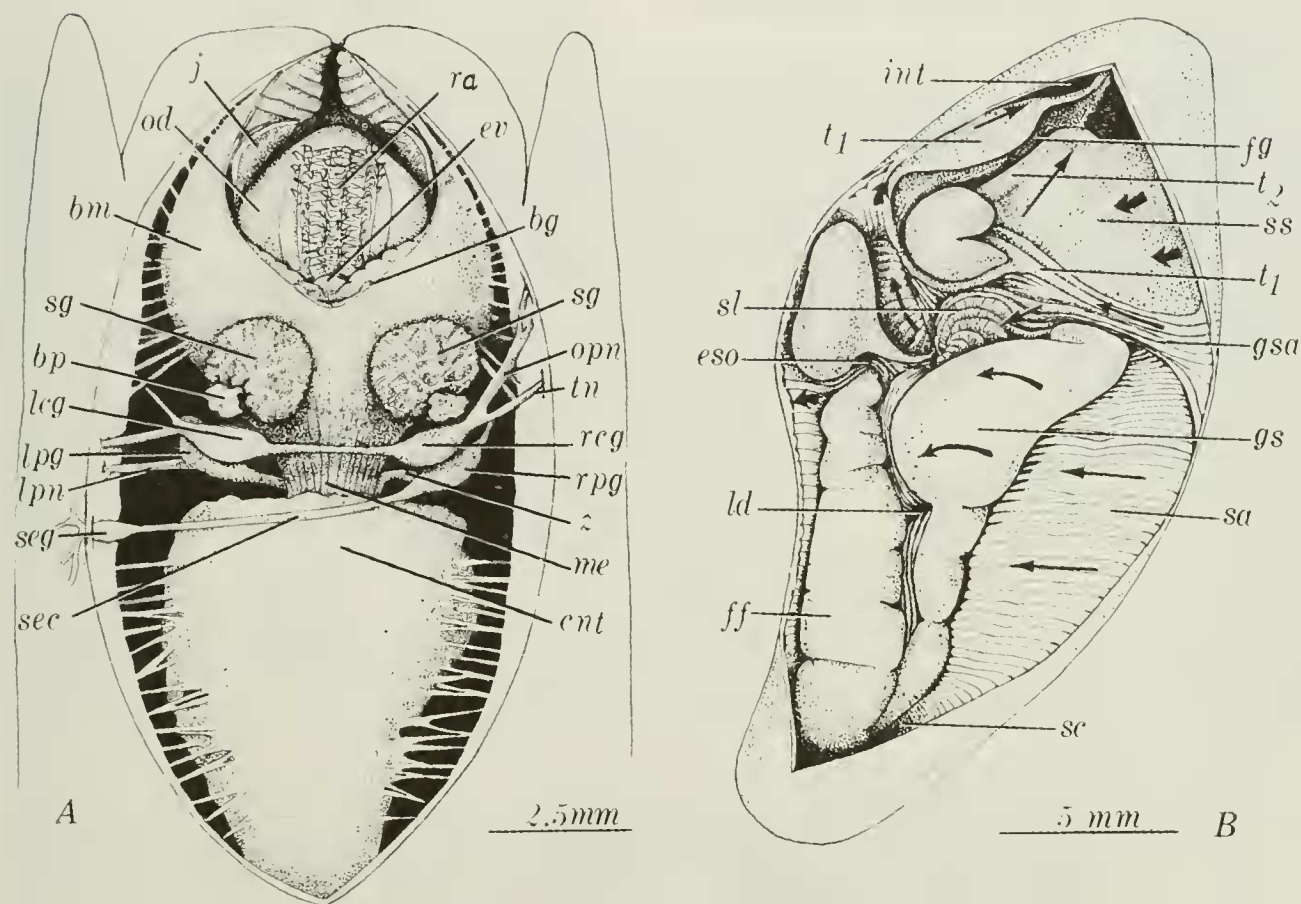


FIG. 5. A, Dissection of head opened by a dorsal longitudinal cut to expose anterior alimentary tract. Connective tissue surrounding nerve ring has been removed. Subesophageal ganglion hidden beneath mid-esophagus. B, Stomach opened by a dorsal longitudinal cut. Arrows indicate direction of ciliary currents. (See Key to Abbreviations, p. 264, for explanation of lettering.)

ated groove may develop during the spawning season.

The foot is moderately small in relation to the shell and has a whitish sole with slight traces of yellow. Quoy & Gaimard's (1834: 107) observations on the color of animals from King George Sound agree with mine. They noted that the underside of the foot was yellowish and striated. I did not see striations in the Point Peron specimens. The entire edge of the sole has a deep ciliated glandular furrow (Fig. 3B, *cf*) that appears to be a pedal gland. It produces mucus, but it was not determined if the gland cells were epithelial or subepithelial. The foot is capable of contraction into numerous, compact transverse folds that appear to secrete mucus in living animals. It is powerful enough to pull the heavy shell enabling animals to partially burrow and even crawl up rocky surfaces.

The large columellar muscle (Fig. 3A-C, *cm*) is very long, comprising 2-3 whorls in a retracted animal. This muscle is white and thick anteriorly but flattens and tapers rapidly

near its proximal origin on the columella of the shell.

Posterior to the mantle cavity is the visceral mass of 6-7 whorls that consists of a large two-lobed kidney (Fig. 3A, *k*), a long stomach (Fig. 3A, *st*) of $1\frac{1}{2}$ whorls and a digestive gland-gonad complex (Fig. 3A, *dg*). The latter has a distinctive banded appearance, clearly seen in both living and preserved snails: at the periphery of each whorl it is light gray while the inner surfaces of the whorls are darker brown, spotted with gray and overlain by a ramose network of white calcium.

The digestive gland is dark brown and is slightly overlain by the gonad in mature animals. Ovaries are externally yellow and consist of tiny spherules located along the periphery of the whorls. The testis is not as easily differentiated from the digestive gland except for a change of external texture along the periphery of the whorl. I did not observe animals during their peak reproductive season; consequently ripe snails may have more conspicuous, characteristic gonads. Gonads

are discussed in more detail in the section on the reproductive tract.

Mantle cavity and associated organs (Figs. 3–4). The mantle cavity is wide and deep. At the base of the left side is a large brown, oval-shaped, bipectinate osphradium (Fig. 3B–C, os; Fig. 4A, os) directly adjacent to the ctenidium. It begins behind the distal end of the ctenidium and closely resembles it in overall morphology, except that the leaflets are wider and more oval. It is referred to by Bouvier (1887b) as the “fausse branchie.” It runs parallel to the ctenidium but does not extend the length of the mantle cavity as in other cerithiaceans. The osphradium is slightly elevated from the mantle skirt on a central axial ridge that bears a series of numerous, flat, bipectinate leaflets. Each of these is attached to the stem of the axis and also fused basally to the mantle skirt. Histological sections show that each leaflet has an external morphology

of numerous parallel ridges that run dorso-ventrally or vertically to the osphradium axis. Cross sections reveal a surface structure covered with ciliated cells and more numerous darkly-stained cells.

The typically monotocardian ctenidium (Fig. 3B, ct; Fig. 4A, ct) is pink and extends most of the length of the mantle cavity to end a short distance from the inhalant pallial siphon. A large, white efferent branchial vessel (Fig. 4B, ebv) lies along the basal length of the left side of the ctenidium.

The thick mantle edge is weakly bilobed, flared and has a slightly scalloped appearance. It consists of an inner row of tiny papillae found only on the upper two thirds of the mantle edge and an outer, continuous, scalloped border (Fig. 3A–B, mp). The scallops are larger on the ventral part of the mantle edge. The deep groove between the two mantle lobes secretes the shell but also traps

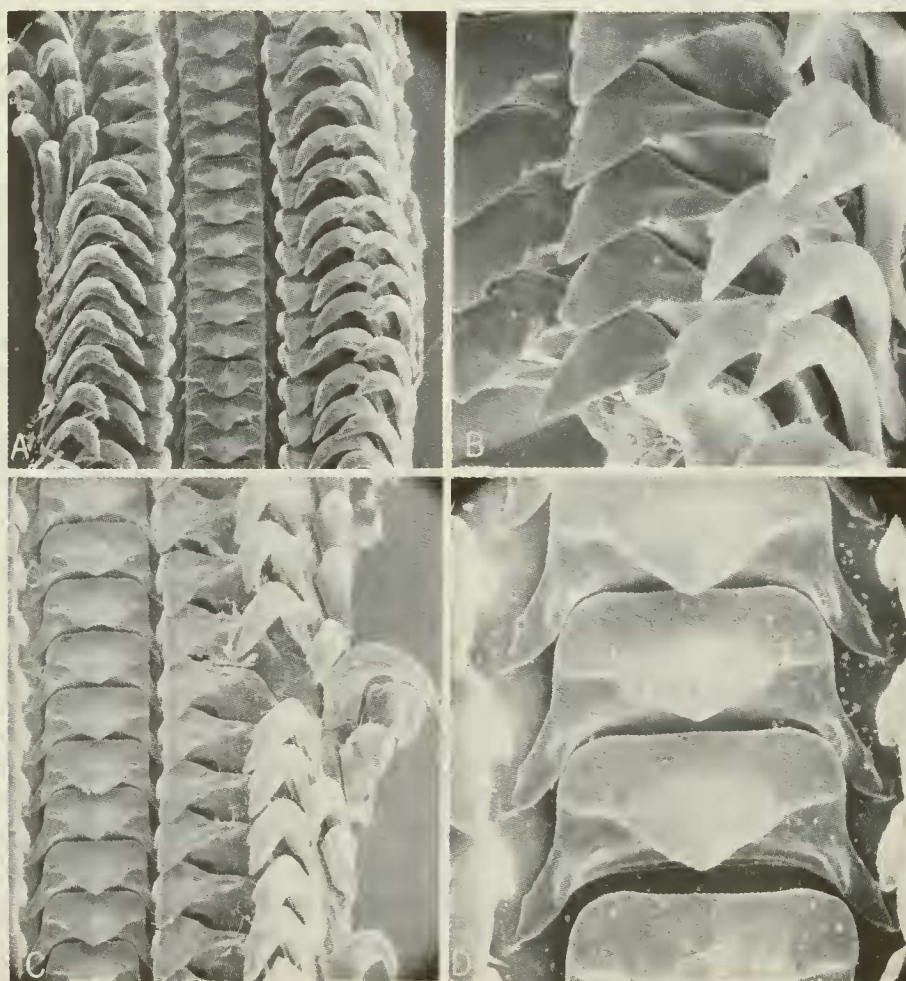


FIG. 6. SEM micrographs of radular ribbon of *Campanile symbolicum*. A, View of central portion of radula showing relationship of various taenioglossate teeth. Radular ribbon is 8.2 mm long and 2.15 mm wide; B, Detail of lateral and marginal teeth, showing tiny cusps adjacent to large cusp of lateral tooth and smooth outer surfaces of inner and outer marginal teeth; C, Enlargement of half row of radular ribbon with marginal teeth folded back showing their insertion on underlying radula membrane; D, Detail of rachidian teeth showing basolateral projections.

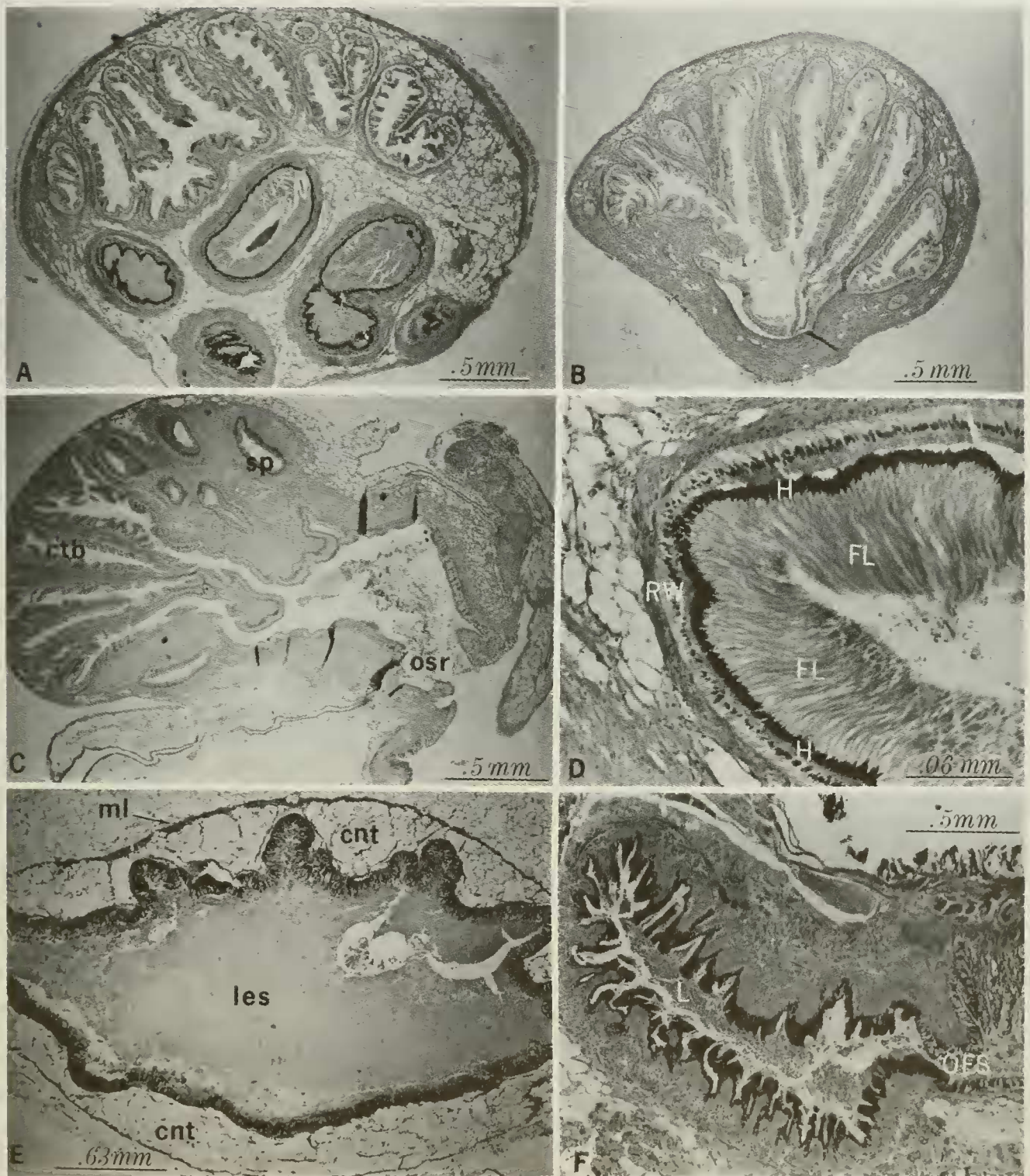


FIG. 7. Histology of reproductive and alimentary tracts. A, Transverse cross section of seminal receptacle, showing network of tubules. Note villous walls of empty tubules at top and smooth walled chambers containing sperm at bottom; B, Longitudinal cross section of seminal receptacle showing connection of tubules; C, Oblique section of seminal receptacle showing opening of duct (osr) leading from seminal receptacle to pallial oviduct; D, Detail of sperm filled chamber in seminal receptacle showing spermatozoans with dark heads (H) oriented along wall of chamber (RW) and flagella (F) projecting into chamber lumen; E, cross section of mid esophagus showing shallow folds in esophagus wall. The lumen (les) is filled with detritus. Note mass of connective tissue (cnt) and thin muscular layer (ml) surrounding esophagus; F, Cross section of esophageal pouch showing deeply folded walls and opening into esophagus (OES).

debris and moves particles by ciliary action from between the mantle and shell. The inhalant siphon (Fig. 3H, *ins*) is thick and comprises a slight fold in the mantle wall, but is not well marked in contrast to the thicker exhalant siphon (Fig. 3A, *exs*).

The hypobranchial gland (Fig. 3A–C, *hg*; Fig. 4A, *hg*) is a large organ, about 6 mm wide, pinkish-tan in color that extends the length of the mantle cavity where it lies between the ctenidium and intestine. It partially covers one half of the intestine, longitudinally, in a thick sheet. The hypobranchial gland begins immediately behind the exhalant pallial siphon and is thus the most anterior of all pallial organs. Its surface is composed of numerous transverse ridges or folds which are papillate along their edges, and most numerous and thin at the rear of the mantle cavity. They become progressively thicker toward the anterior of the snail. The ridges are flocculent in texture and easily fall apart when touched with a probe. The papillate ridges of the hypobranchial gland adjacent and anterior to the anus are thicker and extended into numerous, tiny, flat leaflets (Fig. 4A, *lhg*). The gland in this region is thicker and appears to be slightly different in texture. In cross section, it is separated from the posterior part by a band of tissue that is part of the siphonal musculature. Sections show that it consists mainly of elongate goblet cells and it may produce additional mucus used in conjunction with the exhalant siphon. Its exact function is uncertain. Sections of the hypobranchial gland show that it is composed of elongate, multivacuolated goblet cells that are attached to a basal membrane adjacent to the circular muscular tissue of the mantle wall. Most of the vacuoles appear empty in fixed tissue but some are filled with tiny, darkly stained granules.

The rectum (Figs. 3A, 4A, *r*) is a long, dark brown tube, about 3–4 mm thick that lies between the hypobranchial gland and pallial gonoduct ending near the exhalant siphon. The anal opening (Fig. 4A, *a*) is surrounded by tiny papillae.

The pallial gonoducts lie to the right of the intestine, are open and comprise two laminae which are highly glandular, especially in the female.

Alimentary tract.—The alimentary system of *Campanile* is slightly different from that of most cerithiaceans. One of the notable features is a short, wide, bilobed snout (Fig. 4A, *sn*) that was noted by Bouvier (1877a, b) as a

distinguishing character. The mouth lies at the tip of the snout, recessed between the two lobes that comprise the snout apex. The snout area and head are thick and very muscular.

A pair of large, thick, semilunar-shaped jaws (Fig. 5A, *j*) that are yellowish brown in color and about 5 mm long are inserted in the upper lateral walls of the anterior end of the buccal cavity. The jaws are superficially smooth except for their irregular cutting edges that appear to be formed of numerous transverse rods (Fig. 2d–e). Scanning electron micrographs of the jaws reveal a complex ultrastructure. The free surface of each jaw, exclusive of the cutting edge, is generally smooth but shows concentric lines of growth radiating from the base where the jaw is inserted in the wall of the buccal cavity. The attached surface of each jaw is made up of many microscopic polygonal pits (Fig. 2i). Each pit is about 7 μm in length and its polygonal walls probably conform to individual cell boundaries. Each pit is perforated with numerous tiny holes. The cutting edge of a jaw comprises a matrix of many thin, transverse rod-like structures. In cross section, a jaw is composed of four consecutive layers (Fig. 2h). At the smooth surface is a wide layer of transverse rods and beneath this is another thin layer of transverse rods. Another thin, nondescript layer follows and beneath this a final thick layer of smooth material. It is this final layer that is attached to the wall of the buccal cavity and has the pitted surface. The growing surface of the jaw appears to be the concave portion opposite the cutting edges. The functional significance of the complex ultrastructure of the jaws was not determined.

The buccal mass (Fig. 5A, *bm*) is spherical and attached to the walls of the buccal cavity by numerous tensor muscles that insert onto its entire surface. These are more numerous laterally and ventrally. The odontophoral cartilages (Fig. 5A, *od*) are very large and thick.

The radula (Fig. 6A–D) is stout, moderately short and wide, and about one-tenth the length of the shell. Two radular ribbons from animals with shells about 100 mm in length averaged 8 mm long, 2.25 mm wide and comprised 43 rows of teeth. The rachidian tooth is straight and has a large, plate-like cutting edge comprising a large, broad, triangular cusp flanked on each side by a single, tiny, blunt denticle. The lateral tooth (Fig. 6B–C) is

trapezoid in shape, and has a basal plate with a slight median bulge and a long lateral extension that attaches to the basal membrane. The top is slightly concave and has a cutting edge comprising one small, sharp denticle, a large, platelike triangular, sharp cusp and one to two tiny blunt denticles, consecutively from the inner side. The marginal teeth (Fig. 6B–C) are stout, curved and hook-like with sharp tips and a single denticle on the upper, inner side of each tooth. The bases of the marginal teeth are spatulate where they attach to the basal membrane.

Two yellowish, spherical, loosely-compacted salivary glands (Fig. 5A, *sg*) lie anterior to the nerve ring and lateral and dorsal to the origin of the esophagus. The glands lie close against the nerve ring but do not pass through it. Externally, each of these glands appears to be composed of a matrix of fine tubules. No salivary ducts leading to the oral cavity are visible in gross dissections. Sections of the salivary glands stained blue with Harris' hematoxylin reveal numerous fine tubules comprised of dark-staining secretory cells and lighter, more numerous, highly vacuolated mucoid cells. A salivary duct is embedded in the lateral portion of each gland, adjacent to the buccal mass. The exact point of entry of the salivary ducts into the oral cavity was not determined, but is probably in front of the nerve ring.

Anterior and adjacent to the nerve ring and emerging laterally at the base of the salivary glands is a pair of small, darkly-colored, lobate buccal pouches (Fig. 5A, *bp*). They are connected to the buccal cavity and lie dorso-laterally to it. The buccal pouches are composed of muscular tissue and internally each cavity is highly folded and lined with non-ciliated tissue that comprises a large surface area of tightly packed, dark-staining cells filled with many dark granules (Fig. 7F). Beneath this layer of cells is another layer of more loosely packed cells with simple nuclei that stain pink with Eosin Y indicating an abundance of cytoplasm. The histology (Fig. 7F) of the buccal pouches differs markedly from that of the buccal cavity and anterior esophagus.

Cross sections of the anterior esophagus reveal a deep dorsal food channel and two deep, ventrolateral channels which are all highly folded longitudinally and lined with long cilia. Most of the cells lining the remainder of the anterior esophagus are not ciliated but elongate and goblet-shaped.

At the point where the anterior esophagus

becomes the mid-esophagus (Fig. 5A, *me*) the body cavity is divided by a thin transverse septum lying directly behind the nerve ring. This septum is closely associated with the many muscular elements of the posterior buccal mass and walls of the buccal cavity. It was not clear if this septum completely divides the cephalic hemocoel as does the transverse septum of trochaceans. Its function and exact relationship to the cephalic hemocoel remain uncertain. As the anterior esophagus passes through the nerve ring the food channel and grooves become highly folded and the dorsal food channel seems to disappear directly behind the nerve ring at the point of torsion.

The mid-esophagus is a wide, dorso-ventrally flattened tube that, in comparison with the anterior esophagus, has few longitudinal folds or grooves. The ventral portion of the mid-esophagus is smooth while the dorsal and lateral parts have 4–6 shallow depressions (Fig. 7E). The histology of the mid-esophagus is identical to that of the anterior esophagus only there are more ciliated columnar epithelial cells. The mid-esophagus is buried in a large mass of loosely compacted connective tissue (Fig. 5A, *cnt*) which begins immediately behind the nerve ring where it is thickest. It gradually tapers posteriorly and becomes concentrated to the left of the esophagus. Cross sections of the mid-esophagus show that a thin layer of loose connective tissue (Fig. 7E, *cnt*) surrounds the mid-esophagus for its whole length and it is surrounded by a very thin muscular layer (Fig. 7E, *ml*) which, in turn, is enveloped in more loose connective tissue. The esophagus is thus surrounded by a double layer of connective tissue which histological sections show has no connection or relationship to the interior esophagus. The function of this thin muscular membrane and its relationship to the esophagus and surrounding connective tissue is unknown.

The posterior esophagus is oval to round in cross section, and the wall is folded longitudinally. The interior surface is ciliated, and made up of elongate columnar epithelial cells and few mucus cells.

The stomach (Fig. 5B) occupies 1½ coils of the lower visceral mass and differs markedly from those of other cerithiaceans I have examined in several features. It is a complex structure and difficult to interpret, functionally. Although a style sac (Fig. 5B, *ss*) is present at the intestinal end of the stomach, there is no crystalline style. Freshly collected specimens

I dissected had no trace of a style in their stomachs, but a normal fecal rod or protostyle was present and led into the intestine. *Campanile* lacks a cuticular gastric shield that one sees in other cerithiaceans. Instead there is an elongate raised, non-cuticular muscular area (Fig. 5B, *gs*) and a very complex grooved sorting area (Fig. 5B, *gsa*) lying adjacent to the esophageal opening at the middle of the stomach. The largest portion of the raised muscular area is probably homologous to the area supporting the gastric shield.

If the stomach is opened by a dorsal longitudinal cut, the posterior esophagus (Fig. 5B, *eso*) is seen to open into the stomach at its left mid-section through a circular sphincter muscle. Food passing into the stomach is immediately directed to a large sorting area marked by many latitudinal folds (Fig. 5B, *sa*). From here it moves to a deep grooved channel (Fig. 5B, *gsa*) and into a deep pit lined with glandular tissue that is folded into spirally arranged leaflets (Fig. 5B, *sl*). There are about five major leaflets at the top of the sorting area and many smaller ones leading to the base of the pit. Each leaflet is further folded into longitudinal ridges on each of its sides. The bases of the leaflets are smoother and have fine longitudinal grooves. Ciliary currents move down the longitudinal folds and grooves to the base of each leaflet and thence deeper into the muscular pit of the sorting area. The base of the pit is blind. In the pit of the sorting area are found larger particles and sand grains up to 1.5 mm in diameter.

After sorting, food is probably transferred to the posterior portion of the stomach. This large, white, tapering sac-like area (Fig. 5B, *sc*) lies at the rear of the stomach and is lined with fine transverse folds within which food particles are rotated. The area is probably a vestige of the spiral caecum. Emerging from the caecum is a large flat fold (Fig. 5B, *ff*). At the base of the "gastric shield" is a deep groove leading to the digestive gland (Fig. 5B, *ld*). The muscular walls of the caecal area are thick and internally consist of loose connective tissue interlaced with thousands of fine fibrous muscle strands. Anterior to the large muscular area or gastric shield is a deep ridged groove that leads into the style sac and is bordered at its left by the major typhlosole (Fig. 5B, *t₁*) and on its right by the minor typhlosole (Fig. 5B, *t₂*). The style sac is essentially a smooth area bisected by the major typhlosole and food groove (Fig. 5B, *fg*) leading into the intestine (Fig. 5B, *int*). Tiny, ovoid,

fecal pellets found in the intestine and rectum are held in a fine mucous strand.

Excretory system. The kidney (Fig. 3A–B, *k*) is a large dark brown organ, about 1.5 coils in length. It overlays the end of the mantle cavity and covers part of the albumen gland and much of the pericardium. As it nears the stomach it tapers rapidly and is less thick. The under surface of the kidney is covered by the thin mantle through which may be seen the renal lamellae (Fig. 4B, *rl*). The kidney opening (Fig. 4B, *ko*) is a small slit located at the anterior end near the pericardium and faces the mantle cavity. Another small opening, the renopericardial duct (Fig. 4B, *rpd*), leads from the kidney into the pericardial sac. The part of the kidney bordering the pericardium is lighter in color and looks like a nephridial gland, but sections of this part of the kidney do not show any cellular differences.

An area of distinctive tissue lies adjacent to the rear of the main part of the kidney and extends over the anterior portion of the stomach. It is of a different structure and texture from the kidney and is deeply embedded around the style sac of the stomach. The internal structure is a tubular matrix of fine tiny sacs that are filled with yellowish concretions that are probably waste.

Nervous system. Bouvier (1887b: 149) has described this in great detail and presented accurate figures of it (Bouvier, 1887b: pl. 8, fig. 33). His drawings are difficult to interpret at first glance because he shows the nerve ring with the cerebral commissure cut and the cerebral ganglia reflected back to expose the pleural and subesophageal ganglia.

The cerebral ganglia (Fig. 5A, *l_{cg}*, *r_{cg}*) are above the esophagus posterior to the buccal mass. They are large, elongate and joined by a long cerebral commissure. Four primary nerves emerge anteriorly from each cerebral ganglion and three others run into the walls of the buccal cavity. These innervate the lips, tentacles and eyes and the fourth is the connective to the buccal ganglion (Fig. 5A, *bg*). Each of the pleural ganglia (Fig. 5A, *l_{pg}*, *r_{pg}*) are joined to the cerebral ganglia by very distinct, different connectives. The right pleural ganglion (Fig. 5A, *r_{pg}*) lies close to the right cerebral ganglion and is joined to it by a short, thick connective. The left pleural ganglion differs in lying farther away from the left cerebral ganglion and is joined to it by a long slender connective. A large left pallial nerve (Fig. 5A, *l_{pn}*) emerges from the left pleural ganglion

and runs into the body wall. A long supraesophageal connective (Fig. 5A, *sec*) emerges from the right pleural ganglion, passes over the esophagus and runs into the left body wall where it enlarges to form the supraesophageal ganglion (Fig. 5A, *seg*). This is connected to the left pallial nerve by a moderately long dialyneury. The two pedal ganglia are joined to the cerebral and pleural ganglia by long slender connectives. The pedal commissure is slender and of moderate length. Although I did not see any statocysts, Bouvier (1887b: 149) described them as lying at the posterior base of the pedal ganglia and noted that each statocyst contained numerous statoliths.

At the base of the left pleural ganglion lies the subesophageal ganglion. The connection between these two ganglia is very short and thick and it is difficult to separate the two. The subesophageal ganglion is joined to the right pleural ganglion by a thick zygoneury. There is a long visceral nerve that runs to the visceral ganglia and a typical visceral loop is present.

In summary, the cerebral, pedal and left cerebral-pleural connectives are long, slender and contribute to a "loose" state of the nerve ring. In contrast, condensation of the nerve ring is achieved by the close connection between the left pleural and the subesophageal ganglia, the short, thick connective between the right cerebral and pleural ganglia, and the dialyneury between the pleuro-supraesophageal ganglion and left pallial nerve.

Reproductive system. Males and females have open pallial gonoducts and males are aphyallic. The pallial gonoducts of both sexes are relatively simple and their open condition is best visualized as a slit tube running the length of the mantle cavity, forming dorsal and ventral lobes with the slit facing the mantle cavity. Each lobe comprises an inner and outer lamina (Fig. 3C, *il, ol*; Fig. 4C, *il, ol*) fused together along their axes to the mantle wall. The inner lamina is also fused on its right side to the mantle while the outer lamina is mostly free except for its fused axis. Both laminae are lined internally with numerous transverse glandular folds.

Campanile may be a protandric hermaphrodite because both sexes have a seminal receptacle. This is discussed in more detail later in this paper.

The female pallial duct is larger and more glandular than that of the male. At its proximal left end is an opening that leads to a sac-like

seminal receptacle (Fig. 4B, *sr*) which is unusually placed in that it bulges into the pericardial sac (Fig. 4B, *ps*) although it is histologically distinct from it. The seminal receptacle (Fig. 4A-C, *sr*) is usually a single compact sac but may have several lobes. The interior is a branching series of villous tubes converging at the base of the receptacle (Fig. 7B) to form a single duct that opens to the distal pallial oviduct near the beginning of the albumen gland (Fig. 7C, *osr*). Sections of the seminal receptacle show that the columnar epithelium (Fig. 7B) is ciliated. Sperm are stored in the tubes (Fig. 7A) with the heads (Fig. 7D, *H*) oriented in the walls (Fig. 7D, *RW*) and their flagella (Fig. 7D, *FL*) projecting into the lumen of the tubes. Some tubes did not contain sperm and are more villous than others, as may be seen in a cross section of the receptacle (Fig. 7A, top portion; C, *ctb*). These may function as a bursa.

The pallial oviduct (Fig. 4C) has no sperm collecting gutter, no bursa or spermatophore receptacle and no tubes in the walls of the laminae. The inner surface of each lamina is thrown into transverse folds along its entire length. These folds become yellow, thin, broadly laminate at the proximal end of the oviduct and constitute the albumen gland (Fig. 4A, C, *ag*). Bouvier (1887b: 147), unaware that this was part of the pallial gonoduct, remarked that this area resembled gill leaflets. These leaflets secrete copious amounts of albumen when stimulated. Sections of the albumen gland show large cells with little nuclear material and large vacuoles. The mid (Fig. 4A, *gil*) and distal parts of the pallial gonoduct differ from the albumen gland in having a thick outer lamina of white glandular tissue and probably give rise to the gelatinous portion of the spawn mass. The base of the open oviduct (Fig. 4A, C, *odg*) is lined with fine transverse folds and is densely ciliated. The entire wall of the outer lamina has a median longitudinal furrow (Fig. 4C, *dol*), where the thickness of the wall is reduced so that the free half can be folded over the inner lamina like a baffle to form a physiologically closed tube as in other prosobranchs with an open duct (Fig. 3C, 4C, *b*). The inner lamina is fused on its right side to the body wall and appears comprised of thick, irregular glandular folds on its inner functional surface (Fig. 4A, *gil*).

The male pallial gonoduct is a thinner, more simple open duct and is highly glandular only at its proximal end where it probably functions

as a prostate. The inner lamina is fused on its left side to the body wall as in the female. An opening to a small seminal receptacle occurs in the proximal left end of the pallial gonoduct and leads to a sac-like receptacle that lies within the pericardial sac. It appears to be morphologically identical to the female seminal receptacle. Remains of what appeared to be a disintegrating spermatophore were found in the female oviducal groove; thus, the male pallial gonoduct may also secrete spermatophores, but this needs confirmation. Sections through the testis show typical seminiferous tubules filled with various stages of developing spermatozoans. Sperm extracted from the vas efferens were all eupyrene but my specimens were taken in early winter; thus, spermic dimorphism should be looked for more closely in spring during the height of the reproductive season when animals are seen pairing.

REPRODUCTIVE BIOLOGY

The head-foot region of sexually mature snails becomes pink when they are ripe. This is especially marked in females whose ovaries and eggs are also the same color. The significance of this color in the head-foot is unknown. Pairing was not observed but deposition of spawn begins in September and lasts throughout November (Dr. Robert Black, personal communication). Spawn masses are attached to marine angiosperm grass blades, macroalgae, rocks or other objects on the substratum and are frequently cast up on the beach. Spawn masses seem to be neutrally buoyant.

Eggs are deposited in large jelly-like, crescent-shaped spawn masses (Fig. 8A–B), and closely resemble the spawn of opisthobranchs. An average spawn mass is 175 mm in length, 21 mm wide and 5 mm thick, and contains about 4,000 pink eggs (Table 2). A spawn mass is transparent, free of debris on its surface and viscous throughout. The attachment surface is opaque (Fig. 8A, as) and is located at the base of the mass, usually at one end. The outer covering is very thin, parchment-like and has tiny longitudinal striations. Within the jelly mass the egg capsules, joined by chalazae, appear as a continuous spirally coiled strand (Fig. 8B). There is an average of three eggs per capsule (range 1–5), each about 0.5 mm in diameter. It was not determined if any of the eggs functioned as nurse eggs.

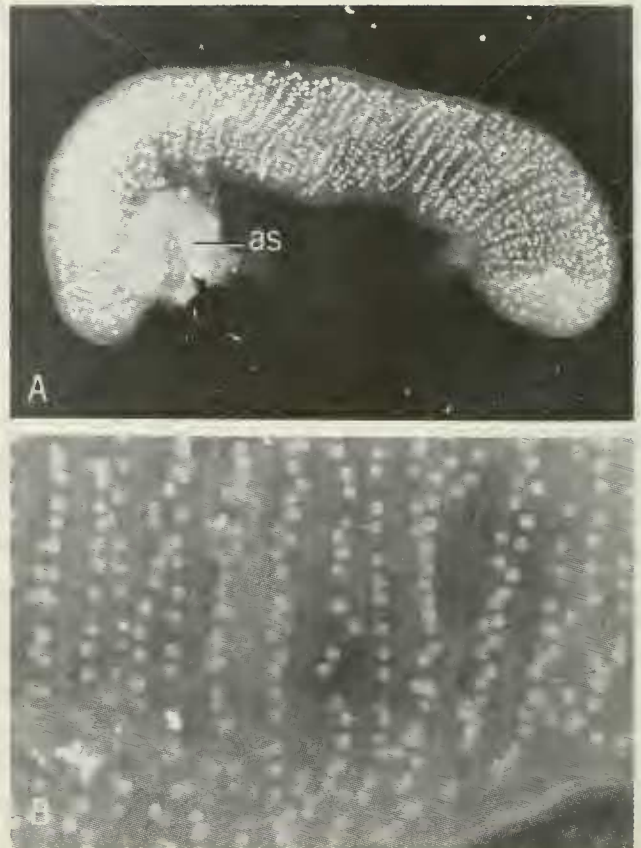


FIG. 8. Spawn of *Campanile symbolicum*. A, Individual spawn mass showing attachment surface (as), 117 mm long; B, Detail of jelly strands and eggs composing spawn mass.

TABLE 2. Statistical summary of spawn measurements of *Campanile symbolicum* (in mm).

Statistic n = 5	Mean	Range	SD
Length	120.2	78–240	66.77
Width	22.4	18–75	2.96
Thickness	4.7	3.8–6.5	1.13
Number of Embryos	4025	3000–6624	1484.2

Embryonic stages ranging from early cleavage to advanced veligers are present within a single spawn mass. Advanced veliger stages have black eyes, small velar lobes, and the embryonic shells (Fig. 2a–c) are smooth, comprise 1½ whorls and lack a sinusigera notch, so typical of mainly planktonic larval shells. A free veliger is unknown, but the advanced state of the late veliger stages and the embryonic shell suggest direct or a short demersal development. Growth of newly hatched snails is rapid (Robert Black, personal communication), but nothing is known of the age of adult snails.

ECOLOGY

Campanile symbolicum normally occurs subtidally in large populations on sandy patches between rocks on limestone reefs. The substratum may have seagrass, macroalgae or may be predominantly sandy. The species is sometimes found in the intertidal zone but the bulk of the population is subtidal. At Pt. Peron, Western Australia, I observed a large population at a depth of 3 m. Animals lie on the sand, sometimes slightly buried, or adjacent to rocky shelves where they are frequently found jammed together. They appear to be inactive during the day with only a few traces in the sand to indicate movement. The species is probably nocturnal because ani-

mals kept in an aquarium were active mostly at night. *Campanile* shells have numerous *Hipponix conicus* (Schumacher) attached to their last two whorls. These are usually on the base of the body whorl adjacent to the siphon or on the outer lip.

The outer lip of adult *Campanile* shells is thin and frequently broken. Crustacean predators can peel back the lip only a short way because it becomes very thick on the penultimate whorl and resists breakage. Moreover, the animals can retract deeply into their shells and thus appear to be safe from predators. No drilled shells were seen.

Fossil records.—*Campanile symbolicum* occurs as a fossil in the Pliocene (George Kendrick, personal communication) and in the



FIG. 9. Geographic distribution of *Campanile symbolicum*.

early Pleistocene (Ludbrook, 1971) of the Eucla Basin of South Australia, although most workers now consider the Eucla Basin to be late Pliocene (Ponder, personal communication). The Pliocene fossil, *Telescopium gigas* Martin, 1881 from Java is very similar to *Campanile symbolicum* and is either conspecific with it or a close relative.

Geographic distribution.—Confined to southwestern Australia.

SYSTEMATICS

Superfamily Cerithiacea Fleming

Family Campanilidae Douvillé, 1904

Diagnosis.—Shell large with chalky surface, elongate, turreted, with straight-sided or slightly convex whorls and moderately incised suture. Body whorl wide and truncate. Growth lines sinuous. Sculpture of suture cords and nodes frequently absent or weak. Aperture narrow and fusiform, anterior canal of moderate length, columella smooth or plaited, periostracum chalky. Operculum ovate, corneous, paucispiral and with eccentric nucleus. Radula taenioglossate, sexes separate, males aphyllid, pallial gonoducts open.

Remarks.—Shell characters, the radula, operculum and open pallial gonoducts of both sexes point to the superfamily Cerithiacea as a proper assignment for this group.

The family Campanilidae was proposed by Douvillé (1904: 311) who later, without explanation, transferred the genus *Campanile* back to the family Cerithiidae Fleming (Douvillé, 1928: 9) and finally regarded it as a subgenus of *Cerithium* Bruguière (Douvillé & O'Gorman, 1929: 362). Most subsequent accounts have ignored the family name and have generally placed *Campanile* in the Cerithiidae. Thiele (1931: 215), Wenz (1940: 771) and Franc (1968: 281) recognized the group as a subfamily, Campanilinae, in the Cerithiidae. Anatomically, *Campanile symbolicum* cannot be referred to the family Cerithiidae and does not fit the limits of any other cerithiacean family. I believe familial status is justified for this group on the basis of a coherent lineage seen in an extensive fossil record, a unique shell structure and physiognomy, and the distinctive anatomical characters described in detail in this paper.

Genus *Campanile* Fischer, 1884

Type-species: *Cerithium giganteum* Lamarck, 1804 [Eocene] (by subsequent designation, Sacco, 1895: 37).

Synonymy

Campanile "Bayle" in Fischer, 1884: 680; Sacco, 1895: 37; Douvillé, 1904: 311; Cossmann, 1906: 71; 1908: 19–27; Boussac, 1912: 19; Iredale, 1917: 325 (in part); Delpey, 1941: 3–5; Cox, 1930: 148–150; Wenz, 1940: 771; Andrusov, 1953: 452; Franc, 1968: 282.

Ceratoptilus Bouvier, 1887a: 36 (type-species, by monotypy, *Cerithium leve* Quoy & Gaimard, 1834); 1887b: 146, pl. 8, fig. 33; pl. 9, fig. 38 (in part).

Campanilopa Iredale, 1917: 325–326 (replacement name for *Campanile*, to be applied to fossil species only) (in part); Delpey, 1941: 20.

Diagnosis.—Shell large, turreted, elongate and with straight-sided whorls or slightly convex whorls and moderately incised suture. Body whorl sharply truncate. Shell with chalky, cancellate outer periostracum that forms a microscopic, pitted surface. Growth lines sinuous. Aperture narrow, fusiform, and at a 45° angle to shell axis. Anterior siphonal canal moderately long, twisted slightly to left. Outer lip thin, smooth and sinuous with an anal notch. Base of outer lip extends over anterior siphonal canal. Columella smooth, concave. Shell sculpture of early whorls comprised of spiral cords and spiral rows of nodules; later whorls usually smooth. Protoconch smooth, 2½ whorls. Operculum ovate, corneous, paucispiral with eccentric nucleus. Radula taenioglossate (2+1+1+1+2). Sexes separate, males aphyllid, pallial gonoducts open, albumen gland large, seminal receptacle projected into pericardium. Spawn comprised of jelly-like strings with large eggs. Ctenidium monopectinate, osphradium short, bipectinate. Pair of salivary glands in front of nerve ring. Stomach complex, without style. Nervous system zygoneurous. Commissures of nerve ring long.

Remarks.—The type-species of this taxon has been the subject of debate. *Campanile* was originally proposed to accommodate a mixed group of large cerithiid-like snails. The name *Campanile* was proposed as a sub-

genus of *Cerithium* by Fischer (1884: 680), who credited the name to Bayle. Fischer's diagnosis was based mainly on conchological characters derived from both the fossil species and from the Recent one, because the operculum is mentioned. Although this diagnosis mentioned the living species first (cited as *Cerithium laeve*) and then cited *Cerithium giganteum* Lamarck, 1804 as a fossil example, a type-species was not designated.

Douvillé (1904: 311) regarded the genus *Campanile* as sufficiently distinct from other cerithiaceans to comprise a separate family and cited *Cerithium laeve* Quoy & Gaimard (= *Campanile symbolicum* Iredale) as representative of the family.

Cossmann (1906: 72), who considered *Campanile* to be a subgenus of *Cerithium* Bruguière, apparently unaware of Sacco's (1895) prior designation of a type-species, selected *Cerithium giganteum* Lamarck. Cox (1930: 148) cited Cossmann's (1906) designation and most other authors have erroneously attributed the selection of the type-species to Cossmann.

Most of the large Tethyan species are characterized by shells with columellar plaits that extend along the entire axis of the shell and have a more nodulose sculpture. In contrast, the living species and a Pliocene fossil, *Cerithium gigas* (Martin, 1881), lack these characters. Cossmann (1906), noting this difference as well as other sculptural and apertural ones, doubted that the living species and its Pliocene fossil homologue from Java should be included together in the same group. He pointed out that there were no fossil representatives of *Campanile* known from the Miocene, implying a broken lineage. He did not, however, propose a new generic name for the group without plaits.

The living species, *Campanile symbolicum* was subsequently referred to the genus *Telescopium* Schumacher by Sowerby (1865; cited as *Cerithium laeve*), who noted that there were essential differences between it and the fossil, *Cerithium giganteum* Lamarck (cited as *Cerithium gigas*, probably in error for *giganteum* because the name *gigas* was proposed in 1881 for a different fossil species).

The soft parts of *Campanile symbolicum* were described by Bouvier (1887a: 36; cited as *Cerithium laeve* Quoy & Gaimard), who realized that this species is anatomically very different from animals in the genera *Cerithium* and *Telescopium*; consequently he proposed

the genus *Ceratoptilus* to accommodate it. Bouvier (1887a, b) was obviously unaware that the name *Campanile* Fischer, 1884, was available. He included the Tertiary fossils in his new genus.

Iredale (1917: 325), also unaware of Sacco's (1895) designation of *Cerithium giganteum* Lamarck as the type-species of *Campanile*, did not accept Cossmann's (1906) designation of this taxon as type-species. Iredale (1917) believed that the name *Campanile* should be restricted to the living species because the original diagnosis of Fischer (1884) employed opercular characters. He stated that *Cerithium giganteum* Lamarck could not be regarded as congeneric because it was, in his opinion, much more like *Terebralia* Swainson, 1840 "in every essential shell character." Iredale (1917) thus excluded the fossil species from *Campanile* and proposed the genus *Campanilopa* for them. It should be noted that Iredale's opinion regarding the type-species is incorrect: had Sacco (1895) not already designated a type-species, Cossmann's (1906) designation of *Cerithium giganteum* Lamarck would be correct, Iredale's (1917: 325; 1949: 20) opinions notwithstanding. The name *Campanilopa* Iredale, 1917, which Iredale applied to the large Tethyan fossils, thus becomes a junior synonym of *Campanile*. *Campanilopa* was regarded as a subgenus of *Campanile* by Delpey (1941: 21) for those fossil species that have columellar plaits. Iredale (1917) was unaware that some of the Tertiary species had smooth columellas and were very much like the Recent *Campanile symbolicum*.

Boussac (1912: 22-23), noting Cossmann's (1906) suggestion that *Cerithium laeve* was probably essentially different from the large fossil *Campanile* species, carefully examined the shells of both groups. He found no essential differences between the Recent species and the fossils and concluded that they were congeneric and should both be assigned to *Campanile*. He did not consider *Campanile* to constitute a family.

Wrigley (1940: 111) concurred with Boussac (1912) and regarded the English Eocene fossil *Campanile* species to be congeneric with the Recent species, *Campanile symbolicum*, from Australia. He was convinced that the sculptural differences did not warrant a generic separation.

Iredale (1949: 20), in a short note, disagreed with Wrigley (1940) and stated that

examination of a series of specimens from Australia convinced him that the Recent species had "nothing whatever to do with the British Eocene fossils." He suggested that the fossils were probably distantly related to the genus *Terebralia* Swainson, 1840.

Delpey (1941) wrote the most comprehensive paper on *Campanile* and presented a thorough history of the nomenclature, tracing the fossil lineage of the group. She delineated the generic characters of *Campanile* and showed that there is considerable interspecific variation in the presence, placement and number of columellar and parietal plaits as well as in shell sculpture. Delpey (1941: 20–21) recognized three subgenera within *Campanile*: *Diozoptyxis* Cossmann, 1896, *Campanilopa* Iredale, 1917 and *Campanile* Fischer, 1884, s.s. She noted that *Campanile gomphoceras* Bayan, 1870, of the Eocene, lacked a columellar plait and closely resembled *Campanile gigas* (Martin) of the Pliocene of Java which she considered to be the direct ancestor of the Recent *Campanile symbolicum*. Delpey (1941) suggested that the genus migrated from the Tethys Sea to Australia and that *Campanile symbolicum* (cited as *Cerithium laeve*) was the modern survivor of a long lineage within the family Campanilidae. She considered the earliest representatives of the group to have arisen from the Nerineidae, a fossil group characterized by elaborate parietal, palatal and columellar folds, and noted the resemblance of some species in the subgenus *Diozoptyxis* to the nerineids. *Diozoptyxis* is not regarded as a nerineid (Sohl, personal communication). Although I do not agree with her about relationships with the nerineids (see Discussion, this paper), her arguments regarding *Campanile* phylogeny appear to be both comprehensive and reasonable. While I do not consider it within my expertise to comment on these speculative relationships, I concur with her conservative classification of the family Campanilidae. In this paper I will deal only with *Campanile symbolicum*, and exclude taxonomic treatment of the fossil species and supraspecific taxa. The question of the generic allocations of the numerous fossil species in relation to the Recent one are beyond the scope of this paper.

Campanile symbolicum Iredale
(Figs. 1–9)

Cerithium leve Quoy & Gaimard, 1834: 106–108; 1833, Atlas, pl. 54, figs. 1–3, non-

binomial (holotype: MNHNP, not registered; type-locality: Port of King George, Australia (= King George Sound, Western Australia) [non *C. laevis* Perry, 1810].

Cerithium truncatum Gray [in] Griffith & Pidgeon, 1834: pl. 13, fig. 1 (error, corrected in Index to *C. laeve* Gray; see Iredale, 1917: 326).

Cerith. leve Quoy [sic], Kiener, 1841: 14–15, pl. 17, fig. 4.

Cerithium laeve Quoy [sic] Deshayes, 1843: 306–307; Sowerby, 1855: 855, pl. 85, fig. 270; Tryon, 1887: 149, pl. 29, fig. 71; Cossmann, 1906: 72–73; Thiele, 1931: 215.

Telescopium laeve (Quoy & Gaimard). Reeve, 1865: pl. 1, figs. 2a, b.

Cerithium (Pyrazus) laeve Quoy [sic]. Kobelt, 1898: 46–47, pl. 10, fig. 1.

Campanile symbolicum Iredale, 1917: 326 (new name); Iredale, 1949: 20; Allan, 1950: 88, pl. 17, fig. 24; Wilson & Gillett, 1971: 32, pl. 12, fig. 1; 1979: 58, pl. 10, fig. 1.

Ceratoptilus laevis (Quoy & Gaimard). Bouvier, 1887a: 37–38; 1887b: 146, pl. 8, fig. 33, pl. 9, fig. 38.

Remarks.—The original species name proposed by Quoy & Gaimard (1834) was spelled "leve" but most subsequent authors have used "laeve." This name is preoccupied by *Cerithium laevis* Perry, 1810, which although slightly different in spelling, does not vary enough to constitute a significant difference (see Code, Article 58), Quoy & Gaimard's name thus becomes a junior primary homonym. In the original description, Quoy & Gaimard (1834: 108) remarked that several hundred individuals were collected in shallow water and that their shells were somewhat similar to those of *Telescopium*, but were longer and had sharper spires. They described the external anatomy of the animals and briefly discussed the internal organs of the mantle cavity. Some notes on the habitat and sexual state of the specimens were presented and the shell, animal and operculum are accurately depicted on pl. 54, figs. 1–3, of the Atlas (Quoy & Gaimard, 1833). Although the Atlas appeared a year earlier than the description, no Latin name was given; consequently the Atlas is non-bionomial.

Iredale (1917: 326) noted that the name *Cerithium leve* was preoccupied and proposed a new name *Campanile symbolicum*, to replace it. Iredale (1917: 326) also pointed out that the name *Cerithium truncatum* Gray, 1834, was an error. Griffith & Pidgeon (1834)

figured the shell under the name *truncatum*, but this was a careless slip and was corrected in the index of the same work.

DISCUSSION

Campanile symbolicum is a relict species representing the end of a long lineage of large mesogastropods in the family Campanilidae. The anatomical evidence derived from the living species places this group within the superfamily Cerithiacea. I agree with Delpey (1941) that this large family probably comprised several genera that underwent a widespread adaptive radiation in the Tertiary. The family is well represented by many fossil species that were abundant in the Tethys Sea and is represented in New World deposits by the endemic genus *Dirocerithium* Woodring & Stenzel, 1959. Woodring (1959) pointed out the Tethyan affinities and also noted the close resemblance of *Campanile gomphoceras* Bayan, 1870, of the European Eocene, to *Dirocerithium*. He also regarded *Bellatara* Strand to be closely related to this lineage. In the Old World the family comprised numerous species in the genera *Diozoptyxis* Cossmann, 1896, *Campanilopa* Iredale, 1917 and *Campanile* Fischer, 1884. It is apparent that the entire fossil assemblage is in need of further revision and study before the composition and lineages within the family can be understood, a task beyond the scope of this paper.

I do not believe that sculptural differences such as placement and number of columellar plaits, between the living species and the fossil taxa warrant a separation of the Recent species from the fossil groups. While the living species may not be congeneric with some of the fossils, it is surely in the same family. It is apparent that the family comprises several supra-specific categories that differ from the living species and future taxonomic studies of the family may show the need for a new genus to accommodate the Recent form. In this paper I prefer to be conservative and refer the living species to the genus *Campanile*.

The shell of the living species does not differ substantially from that of the fossils (see Delpey, 1941) and present understanding of plate tectonics provides sufficient explanation for the linkage between the Tethyan fossils and the living species in southwest Australia without having to invoke any farfetched migration theories.

The pitted surface of Eocene *Campanile*

fossils noted by Wrigley (1940: 111) resembles the pattern seen on the thick, calcified periostracum or "intrinsic" of the living species. I suggest that the pits on the fossils are periostracal in origin and that this is probably a family character.

Delpey (1941) noted that some of the fossil campanilids with elaborate parietal, palatal and columellar folds closely resembled members of the Nerineidae and suggested that the Campanilidae arose from the nerineid lineage. This is most unlikely because nerineids have heterostrophic protoconchs and deep anal sulci and are considered to be in the subclass Euthyneura (Taylor & Sohl, 1962: 11, 16–17). Thus, any resemblance between these two groups is due to convergence and does not imply relationship.

Both the living species and the fossil taxa have been referred to genera within the family Potamididae Fleming by Sowerby (1865) and Iredale (1917: 1949) but I do not concur. The ecology and anatomy of *Campanile* differ substantially from those of the amphibious potamidids which have multispiral, circular opercula, differently arranged open pallial gonoducts, thin, ridge-like osphradia and long snouts with radulae that frequently bear basal cusps.

The elongate, multi-whorled shell, the apertural physiognomy, corneous operculum, taenioglossate radula, aphyllid males and open pallial gonoducts in both sexes are conservative characters found in nearly all cerithiaceans; however, the combined anatomical features of sensory, reproductive, alimentary and nervous systems of *Campanile* are, as far as is known, unique among the Cerithiacea and support its allocation to a separate family, the Campanilidae. A discussion of these unique anatomical features and speculation about the phylogenetic relationship of *Campanile* to other higher cerithiacean taxa follows.

The external anatomy of *Campanile* differs from that of other cerithiaceans in several features: *Campanile* has a deep ciliated pedal gland around the edge of the entire sole of the foot (Fig. 4B, cf) whereas in cerithiids and some potamidids there is only a propodial furrow. In a few potamidids there is a centrally placed pedal gland. The entire mantle edge of *Campanile* has papillae on it, although these are reduced ventrally (Fig. 3A–B, mp), while in the cerithiids the ventral part of the mantle edge is always smooth. In vermetids and pleurocerids, the entire mantle edge is smooth and in the turritellids completely

papillate; while in the thiarids the condition is mixed, depending upon the genus or species. The short, thick snout of *Campanile*, noted by Bouvier (1887b), differs from that of most other cerithiids which have longer and more extensible snouts.

The columellar muscle of *Campanile* is unusual among cerithiaceans in that it is unusually long and forms a long prominence at its proximal end (Fig. 3A–B, *cm*). This may enable the animal to withdraw more deeply into its shell. A similar columellar muscle has been depicted by Morton (1965) and Hughes (1978) for the members of vermetid genera *Vermetus*, *Serpulorbis*, *Dendropoma* and *Petalococonchus*, all capable of deep withdrawal into their shells.

The short, oval, bipectinate osphradium (Fig. 4A, *os*) differs from those of all other known cerithiaceans and most mesogastropods where the osphradium is normally a long slender structure that traverses the length of the mantle cavity adjacent to the ctenidium. Other mesogastropods with a short bipectinate osphradium include members of the Cypraeacea, Calyptraeidae, and the genera *Velutina* and *Balcis*. In *Campanile*, the osphradium is unusual in that it is placed anteriorly in the mantle cavity, and both its placement and anatomy are identical to those seen in most neogastropods.

The extension of the hypobranchial gland and its modification by folding into tiny leaflets adjacent to the anus (Fig. 4A, *lhg*) are anatomical features unrecorded for other cerithiaceans. The presence of numerous elongate goblet cells in this tissue testifies to its secretory ability. It may produce additional mucus to bind fecal pellets as they pass out the exhalant siphon and down the ciliated groove on the right side of the foot.

The pallial oviduct of *Campanile* is simple in comparison to those of the cerithiids, modulids, turritellids and vermetids in that the laminae comprising it lack the internal tubes and bursae associated with spermatophore retention and sperm transfer. Instead, the pallial oviduct is a simple slit tube (Fig. 4C), but one in which the transverse interior folds of the distal end of the laminae are elaborated into rounded filaments forming a large albumen gland (Fig. 4A, *ag*) unlike anything seen so far in other cerithiaceans. As seen earlier, the spawn mass produced by the animal is quite large and gelatinous (Fig. 8A–B) and it is possible that this gland and the mid-glandular part of the oviduct contribute to its formation.

One of the more unusual features of *Campanile* reproductive anatomy is the presence of a sac-like seminal receptacle that bulges into the pericardial sac (Fig. 4A–B, *sr*, *ps*). I know of nothing else like this in any cerithiacean, although several rissoacean species store sperm in the pericardium (Ponder, personal communication). The arrangement is rare among prosobranchs. There is convincing anatomical evidence to suggest that *Campanile* is a protandric hermaphrodite. A seminal receptacle is present at the proximal left side of the pallial gonoduct in both sexes but is more fully developed in females where it may consist of several lobes. It appears that larger individuals are females and smaller ones males. Sections of the gonads of larger snails revealed only developing ova while those of smaller animals clearly showed seminiferous tubules filled with varying stages of developing spermatozoans. Although I found no histological evidence of simultaneous hermaphroditism, transitional stages between sexes should be looked for by future workers.

Sections of the seminal receptacle (Fig. 7A, D) show that the branching chambers containing oriented sperm have relatively smooth walls (Fig. 7A, lower chambers; Fig. 7D, C, *sp*), while the empty chambers are villous and ciliated (Fig. 7A, upper chambers; C, *ctb*). The receptacle thus appears to be divided into two kinds of interconnected branching chambers. The empty tubes and chambers may assist in sperm transport, but their exact function remains undetermined.

Another unusual aspect of *Campanile* reproductive biology is the bright pink color of the head-foot in ripe animals, particularly females. I know of no other cerithiacean in which this phenomenon has been recorded and its significance is unknown.

The presence of what appeared to be a disintegrating spermatophore in the pallial oviduct needs reconfirmation; however, most cerithiaceans such as the cerithiids, modulids and vermetids produce spermatophores. If *Campanile* has only eupyrene sperm, it is unusual because all cerithiaceans heretofore studied show spermic dimorphism.

The spawn of *Campanile* (Fig. 8A–B) are unusual because of their large size, high gelatinous content, the lack of individual hyaline capsules for each egg and the presence of a chalaza connecting the egg capsules. The spawn resemble those of opisthobranchs and polychaetes more than those of

prosobranch spawn. Robertson (1976: 231) pointed out that chalazae are characteristic of opisthobranchs and primitive pulmonates, but among the prosobranchs are known only in the genus *Valvata* and in members of the Architectonicidae, which are not typical of the group. The connections between egg chambers in *Campanile* may not be truly homologous with the chalazae of opisthobranch spawn. The presence of eggs within mucous capsules rather than hyaline capsules is also unusual and the fact that several eggs may be in an individual capsule points to the possibility of nurse eggs. While the high number of eggs per spawn mass and moderate size of individual eggs would seem to indicate indirect development, the developmental mode appears to be direct or demersal. Evidence for non-pelagic development is strong: advanced veliger stages with tiny velar lobes were observed in preserved spawn and the embryonic shell (Fig. 2a-c) is smooth, bulbous, lacks a sinusigera notch and has only one and a half whorls.

All of the above observations raise more questions and it is obvious that more careful work on the developmental biology of *Campanile* is needed.

While most cerithiid jaws are thin and consist of many tiny, flat plates, those of *Campanile* (Fig. 2d-e, h-i) are very thick and structurally complex, as outlined previously. The significance of this difference is unclear, but their structure is undoubtedly related to their ontogeny and needs further detailed study. The typically taenioglossate radula (Fig. 6A-D) is short in comparison to the size of the animal and has fewer rows of teeth than the radulae of other cerithiids which are much smaller animals than *Campanile*. This is peculiar because most snails that graze on coarse substrates, as does *Campanile*, have long radular ribbons. The radula of *Campanile*, however, is wide and robust and cusps of the anterior rows of teeth are only slightly worn.

The thin septum behind the nerve ring that divides the cephalic hemocoel of *Campanile* is more anterior than the transverse septum of trochids which lies where the mid-esophagus joins the posterior esophagus (Fretter, in litt.).

The paired salivary glands and their ducts lie anterior to the nerve ring (Fig. 5A), as in the cerithiids, modulids (Houbrick, 1980), vermetids (Morton, 1951: 29) and in nearly all rissoids (Davis et al., 1976: 276; Ponder, personal communication). This is further documentation that the location of salivary

glands and their ducts is a variable feature among the mesogastropods.

The presence of paired buccal pouches (Fig. 5A, bp) in *Campanile* is noteworthy, because they are unknown among other cerithiaceans. I previously thought that the salivary glands of *Cerithium* were buccal pouches and stated that their ducts passed through the nerve ring, but this was erroneous (Houbrick, 1974: 43). Although found in littorinids, it appears that the cerithiids, modulids, vermetids and turritellids all lack buccal pouches. It is interesting to note that buccal pouches and anterior salivary glands are required for neogastropod ancestors.

The mid-esophagus loses all traces of the dorsal and ventral food channels but is unusual in having shallow lateral folds (Fig. 7E). *Campanile* differs from anatomically known cerithiids and modulids in lacking an esophageal gland, but the vermetids and turritellids known also lack this gland. Although it is not uncommon for gastropods to have loose connective tissue surrounding the esophagus, the mass of loose connective tissue that surrounds the mid-esophagus of *Campanile* (Fig. 7E, cnt) is unusually large and noteworthy. Although this tissue superficially looks like an esophageal gland, sections show that it has no glandular elements or connections with the esophagus. A further distinction of this region is the thin muscular sheet in the middle of the connective tissue surrounding the mid-esophagus (Fig. 7E, ml). The function of this loose connective tissue and its thin muscular sheet was not determined.

The stomach of *Campanile* has a well-developed style sac (Fig. 5B, ss), but a cuticular gastric shield is lacking, and I was unable to find any trace of a style, even in freshly collected animals. It is possible that a style is present only at certain times, as in some bivalves. One of the most unusual features of the stomach is the series of leaflets spirally arranged in a deep pit located in the sorting area (Fig. 5B, sl). Although I have seen a similar structure in the stomach of *Gourmya gourmyi* (Crosse), which is a cerithiid snail, I know of no structure like this in any other prosobranchs with the exception of the volute *Alcithoe*, for which Ponder (1970: 19) described similar gastric leaflets. In *Alcithoe*, they are arranged in parallel rows rather than in a spiral pit, but the structure and ciliary currents of each leaflet are the same. Ponder noted that they are an efficient sorting device in a relatively uncomplicated stomach; this is

in direct contrast to the complex stomach of *Campanile*. The pit and leaflets probably deal with the larger particles and this is a modification from other cerithiaceans. The posterior of the stomach, which I interpret as the vestige of a spiral caecum, is another distinctive structure (Fig. 5B, sc). Reduced spiral caeca have been recorded in other mesogastropods, such as some turritellids, cerithiids and calyptraeids, by Fretter & Graham (1962: 224) but in *Campanile* this structure is much larger and more conspicuous.

A mixture of loose and condensed neural elements including dialyneury and zygoneury exists in *Campanile*. It is difficult to assess the significance of this arrangement of the nervous system because not enough is known of other cerithiacean nervous systems to make meaningful comparisons with *Campanile*.

As seen in the foregoing discussion, *Campanile* falls well within the cerithiacean anatomical groundplan but the relationship of the Campanilidae to other cerithiacean families is more difficult to assess. It appears to be closest to the Potamididae and Cerithiidae in general physiognomy and ecology, but is probably related to them only distantly. There are several anatomical features of *Campanile* that are reminiscent of neogastropods. Among these are the short, distally located bipectinate osphradium, anterior position of salivary glands and ducts relative to the nerve ring, and the complex spirally arranged leaflets in the sorting area of the stomach although the latter are not typical of neogastropods. The presence of a calcified periostracum or intritacalx is known in some rissoids and epitioids but is not common in mesogastropods. Although I do not believe that these features indicate a relationship between *Campanile* and the neogastropods, they are unusual and set this group apart from other cerithiaceans and most mesogastropods.

The Campanilidae is an old family as are other cerithiacean marine families such as the Cerithiidae, Potamididae, Vermetidae, Turritellidae, Dialidae, Cerithiopsidae, and the Modulidae. All these families were present in the late Cretaceous and appear to have undergone little change in basic shell form since then. The cerithiaceans appear to constitute a large monophyletic assemblage. All share the basic primitive anatomical traits of open pallial gonoducts and aphyllid males and are algal-detrital feeders with taenioglossate radulae and complex stomachs.

Nearly all members of the group have a crystalline style.

In general, each cerithiacean family has radiated into a distinctive spatial, trophic niche. It is obvious that the success of many families is due to basic morphological innovations in shell and soft parts or to physiological modifications that led to new adaptations in feeding and exploitation of new habitats such as the estuarine and fresh-water biotopes. Other modifications have occurred in the reproductive systems (spermatophores, spermatozeugma, dimorphic sperm, complex ducts in open pallial gonoducts, brooding chambers), but the adaptive significance of these modifications is not always clear. A brief summary of the major cerithiacean families and their ecological niches follows.

The Turritellidae, characterized by long coiled shells, is an abundant subtidal group of animals that tend to live on soft substrata where they are detrital-filter feeders (Graham, 1938; Fretter & Graham, 1962). The Vermetidae is an intertidal to subtidal, sessile group of snails with uncoiled shells usually found on hard substrata feeding on detritus by ciliary mechanisms and mucous nets (Morton, 1965; Hadfield, 1970; Hadfield et al., 1971; Hughes, 1978). The Potamididae comprise a large group of intertidal estuarine amphibious snails with turreted shells that are grazers on algae and detritus. They are frequently large animals and are common in tropical mangrove habitats, salt marshes and muddy environments. The Cerithiidae are a large, complex family of intertidal to subtidal snails with turreted shells common in tropical areas. This group is primarily composed of algal-detritus feeders and has radiated into a variety of habitats including coral reefs, rocky beaches, sandy lagoons, mud flats and grass beds (Houbrick, 1974; 1978). The Pleuroceridae, regarded as the freshwater branch of the Cerithiidae, comprises a large family of turreted snails that live in well-oxygenated water in temperate and tropical regions (Morrison, 1954). The Dialidae, Litiopidae, and Diastomidae are little known families, the former comprising small snails common in tropical areas and the latter a largely extinct group of larger snails with turreted shells and with only one living species. The Modulidae is a small family of subtidal snails with trochoid shells that live in grass beds or on coral reefs (Houbrick, 1980). The Planaxidae is a small group of tropical snails that live in the rocky intertidal and brood their

young in special incubation chambers in the head (Ponder, 1979). The Thiaridae, a large family of freshwater snails, tend to be parthenogenetic and ovoviviparous and are thought to be derived from the marine Planaxidae (Morrison, 1954). The Cerithiopsidae are small multispined snails that have an acrembolic proboscis (Fretter, 1951) and feed on sponges. They are no longer considered cerithiaceans (Fretter, 1979).

The major adaptive radiations of cerithiacean marine families occurred at the end of the Cretaceous and it is not at all clear from the fossil record or from our knowledge of anatomy how these groups are related to each other. The Campanilidae stands apart from the other families in some aspects of anatomy and is also noteworthy because of the large size attained by many of its members. Although it is not uncommon for some species of other cerithiacean families such as the Turritellidae, Vermetidae, Potamididae and Cerithiidae, to be large animals, the Campanilidae developed this trait to an extraordinary degree.

These large snails were most common in the early Tertiary when they seem to have reached an evolutionary peak in number of species. Members of the Campanilidae probably played the same ecological role in Tethyan shallow water ecosystems as Recent Strombidae in similar contemporary habitats. They undoubtedly were feeders on epiphytic algae and occupied the same trophic niche as do large snails of the living strombid genera *Strombus*, *Lambis* and *Tibia*.

The Strombidae became established in the late Eocene to early Miocene and flourished during the Pliocene and early Pleistocene (Abbott, 1960: 33). Competition with this trophically similar group of large snails probably led to the diminution in species of the Campanilidae. The living survivor, *Campanile symbolicum*, is now confined to southwest Australia where only one small strombid species occurs, *Strombus mutabilis* Swainson (Abbott, 1960: 74). It is noteworthy that southern Australia harbors several other Tethyan relicts, the monotypic gastropod *Neodiatostoma melanooides* (Reeve), family Diastomidae, and the bivalve *Neotrigonia*, family Trigoniidae, although the latter lives all around Australia.

The actual reasons for the virtual extinction of the Campanilidae are unknown, but sea level changes and fluctuating temperatures

associated with the closure of the Tethys Sea undoubtedly placed additional stress on this group of remarkably large gastropods.

ACKNOWLEDGMENTS

I am indebted to Dr. Fred Wells of the Western Australian Museum, Perth, for his kind assistance and for the use of laboratory space and a vehicle for field work during my stay there. I also thank Ms. Miriam Rogers for her help in collecting specimens and for processing field material.

For examination of specimens in their charge I thank Dr. George Davis, Academy of Natural Sciences of Philadelphia, Dr. William K. Emerson, American Museum of Natural History, Dr. Brian Smith, National Museum of Victoria, and Dr. Winston Ponder, The Australian Museum, Sydney.

I thank Dr. Robert Black of the University of Western Australia for sending me preserved samples of spawn and for information about spawning.

Histology was done at the Smithsonian Institution's Fort Pierce Laboratory. I thank Dr. Mary Rice for her kind assistance in using this facility, and Mrs. June Jones for typing the original draft of this paper. The scanning electron micrographs were supplied by the Smithsonian Scanning Electron Microscope Lab. All other photography was done by Mr. Victor Krantz of the Smithsonian Photographic Services.

This research was accomplished with the aid of a Smithsonian Research Award.

I thank Dr. Winston Ponder and Dr. Vera Fretter for critically reading the first draft of this paper.

LITERATURE CITED

- ABBOTT, R. T., 1960, The genus *Strombus* in the Indo-Pacific. *Indo-Pacific Mollusca*, 1: 33-146.
- ALLAN, J., 1950, *Australian Shells*. Melbourne, 487 p., 44 pl.
- ANDRUSOV, D., 1953, Nové Paleontologické Nálezky v Karpatskom Paleogéne. *Geologický Sborník Slovenskej Akadémie vied*, 4: 431-496, pl. 71-74.
- BAYAN, F., 1870, Sur les terrains tertiaires de la Vénétie. *Bulletin de la Société Géologique de France*, ser. 2, 27: 444-486.
- BOUSSAC, J., 1912, Essai sur l'évolution des Cérithidés dans le Mésonummulitique du Bas-

- sin de Paris. *Annales Hébert. Annales Stratigraphie et de Paléontologie du Laboratoire de Géologie de la Faculté des Sciences de l'Université de Paris*, 6: 1-93, 16 pl.
- BOUVIER, E. L., 1887a, Observations sur le genre *Ceratoptilus* créé dans la famille des Cérithidés. *Bulletin de la Société Philomathique de Paris*, ser. 7, 11: 36-38.
- BOUVIER, E. L., 1887b, Système nerveux, morphologie général et classification des Gastéropodes, prosobranches. *Annales des Sciences naturelles*, ser. 7, 3: 1-510.
- COSSMANN, M., 1896, Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris faisant suite aux travaux Paleontologiques de G. P. Deshayes. *Annales de la Société Royale Malacologique de Belgique*, 31: 1-94, 3 pl.
- COSSMANN, M., 1906, *Essais de Paléoconchologie Comparée*, 7: 248 p. Paris.
- COSSMANN, M., 1908, A propos de *Cerithium cornucopiae* Sow. *Mémoire de la Société Linnéenne de Normandie*, 23: 19-27, pl. 2.
- COX, L. R., 1930, Mollusca of the Hangu Shales. *Palaeontologica Indica*, new ser. 15: 129-121, pl. 17-22.
- DAVIS, G. M., KITIKOON, V. & TEMCHAROEN, P., 1976, Monograph of "*Lithoglyphopsis*" *aperta*, the snail host of Mekong River Schistosomiasis. *Malacologia*, 15: 241-287.
- DELPEY, G., 1941, Histoire du Genre *Campanile*. *Annales de Paléontologie*, 24: 3-25.
- DESHAYES, G. P., 1843, In: LAMARCK, *Histoire Naturelle des Animaux sans Vertèbres . . .*, ed. 2, 9: 728 p.
- DOUVILLE, H., 1904, Mollusques Fossiles, In: MORGAN, J. DE, *Mission Scientifique en Perse*, Vol. 3, *Études Géologiques*, part 4, *Paléontologie*: 191-380, pl. 25-50.
- DOUVILLÉ, H., 1928, Les couches à *Cardita beaumonti*. *Memoirs of the Geological Survey of India. Palaeontologia Indica*. new ser., 10: 1-25, 4 pl.
- DOUVILLÉ, H. & O'GORMAN, 1929, L'Éocène du Bearn. *Bulletin de la Société Géologique de France*, ser. 4, 29: 329-390, pl. 29-32.
- FISCHER, P., 1884, *Manuel de Conchyliologie et de Paléontologie Conchyliologique*. Paris, p. 609-688.
- FRANC, A., 1968, Classe des Gastéropodes (Gastropoda Cuvier, 1798). In: GRASSÉ, P. O. (ed.), *Traité de Zoologie, Anatomie, Systématique Biologie*, Vol. 5, *Mollusques Gastéropodes et Scaphopodes* (Fascicule III), Paris, 1083 p.
- FRETTER, V., 1951, Observation on the life history and functional morphology of *Cerithiopsis tubercularis* (Montagu) and *Triphora perversa* (L.). *Journal of the Marine Biological Association of the United Kingdom*, 29: 567-586.
- FRETTER, V., 1979, The evolution of some higher taxa in gastropods. In: *Symposium on the Biology and Evolution of Mollusca*, Sydney, Australia (unpublished mimeographed abstract).
- FRETTER, V. & GRAHAM, A., 1962, *British Proso-*
- branch Molluscs, their Functional Anatomy and Ecology*. Ray Society, London, 755 p.
- GRAHAM, A., 1938, On a ciliary process of food-collecting in the gastropod *Turritella communis* Risso. *Proceedings of the Zoological Society of London*, 108: 453-463.
- GRAY, J. E. See GRIFFITH & PIDGEON, 1834.
- GRIFFITH, E. & PIDGEON, E., 1834, *The Mollusca and Radiata*. In: CUVIER, *The Animal Kingdom*, 12: 601 p., 20 pl. London.
- HADFIELD, M., 1970, Observations on the anatomy and biology of two California vermetid gastropods. *Veliger*, 12: 301-309.
- HADFIELD, M., KAY, E. A., GILLETTE, M. U. & LLOYD, M. C., 1971, The Vermetidae (Mollusca: Gastropoda) of the Hawaiian Islands. *Marine Biology*, 12: 81-98.
- HOUBRICK, R., 1974, The Genus *Cerithium* in the western Atlantic. *Johnsonia*, 5(50): 33-84.
- HOUBRICK, R., 1978, The Family Cerithiidae in the Indo-Pacific. Part 1: The Genera *Rhinoclavis*, *Pseudovertagus* and *Clavocerithium*. *Monographs of Marine Mollusca*, No. 1: 130 p.
- HOUBRICK, R., 1980, Observations on the anatomy and life history of *Modulus modulus* (Prosobranchia: Modulidae). *Malacologia*, 19: 117-142.
- HUGHES, R., 1978, The biology of *Dendropoma corallinaceum* and *Serpulorbis natalensis*, two South African vermetid gastropods. *Zoological Journal of the Linnean Society*, 64: 111-127.
- IREDALE, T., 1917, More molluscan name changes, generic and specific. *Proceedings of the Malacological Society of London*, 12: 322-330.
- IREDALE, T., 1949, Western Australian Mollusks. *Proceedings of the Royal Zoological Society of New South Wales*, 1947-1948, p. 18-20.
- KIENER, L. C., 1841(-1842), *Spécies général et iconographie des coquilles vivantes*. Genre Cérîte. Paris, 5: 104 p., 32 pl.
- KOBELT, W., (1888-)1898, Die Gattung *Cerithium*, 297 p., 47 pl. In: MARTINI, F. H. W. & CHEMNITZ, J. H., *Neues systematisches Conchylien-Cabinet . . .* 1(26). Nurenburg.
- LAMARCK, J., 1804, Suite des mémoires sur les fossiles des environs de Paris. *Annales du Muséum National d'Histoire Naturelle*, 3: 436-441.
- LUDBROOK, N., 1971, Large gastropods of the families Diastomatidae and Cerithiidae (Mollusca: Gastropoda) in southern Australia. *Transactions of the Royal Society of South Australia*, 95: 29-42, 6 pl.
- MARTIN, K., 1881, Tertiaer-Versteinerungen von Östlichen Java. *Sammlungen des Geologischen Reichsmuseums in Leiden*, 1: 105-130, pl. 6-8.
- MORRISON, J. P. E., 1954, The relationships of old and new world Melanians. *Proceedings of the United States National Museum*, 103: 357-394.
- MORTON, J. E., 1951, The structure and adaptations of the New Zealand Vermetidae. *Transactions of the Royal Society of New Zealand*, 79: 1-51.
- MORTON, J. E., 1965, Form and function in the

- evolution of the Vermetidae. *Bulletin of the British Museum (Natural History)*, 11: 585–630.
- PERRY, G., 1810(–1811), *Conchology: or the Natural History of Shells* . . . London, 61 pl. + text.
- PONDER, W. F., 1970, The morphology of *Alcithoe arabica* (Gastropoda: Volutidae). *Malacological Review*, 3: 127–165.
- PONDER, W. F., 1979, Cephalic brood pouches in *Planaxis* and *Fossarus* (Fossaridae and Planaxidae, Cerithiacea, Gastropoda). Unpublished abstract in program for *Symposium on the biology and evolution of Mollusca*, Sydney, Australia, May, 1979.
- QUOY, J. R. C. & GAIMARD, J. P., (1833–)1834, *Voyage de decouverts de l'Astrolabe executé par ordre du Roi pendant les années 1826–1827–1828–1829 sous le commandement de M. J. Dumont D'Urville*. *Zoologie*, 3: 1–366 + Atlas (1833), 93 pl.
- RADWIN, G. & D'ATTILIO, A., 1976, *Murex Shells of the World. An Illustrated Guide to the Muricidae*, 284 p., 32 pl., illustrated. Stanford.
- REEVE, L. A., 1865, *Conchologia Iconica: or illustrations of the shells of molluscos animals*. Vol. 15, *Cerithium*, 20 pl. + index. London.
- ROBERTSON, R., 1976, Marine Prosobranch Gastropods: Larval Studies and Systematics. *Thalassia Jugoslavica*, 10(1–2): 213–238.
- SACCO, R., 1895, In: BELLARDI, L., *I Molluschi dei Terreni Terziarii del Piemonte e della Liguria*. Parte XVII (*Cerithiidae*, *Triforidae*, *Cerithiopsidae* e *Diastomidae*), 83 p., 3 pl.
- SOWERBY, G. B., 1855, *Thesaurus Conchylorum, or monographs of genera of shells*, Vol. 2, *Cerithium*: 847–859, pl. 176–186. London.
- SOWERBY, G. B., 1865, In: REEVE, L. A., *Conchologia Iconica: or illustrations of the shells of molluscos animals*. Vol. 15. London.
- SWAINSON, W., 1840, *A Treatise on Malacology or the Natural History of Shells and Shellfish*, 419 p. London.
- TAYLOR, D. W. & SOHL, N., 1962, An outline of gastropod classification. *Malacologia*, 1: 7–32.
- THIELE, J., 1929, *Handbuch der systematischen Weichtierkunde*. Fischer, Jena. Vol. 1, part 1, 376 p.
- TRYON, G. W., 1887, *Manual of Conchology; structural and systematic; with illustrations of the species*. ser. 1, 9: *Cerithium*, p. 127–149, pl. 20–29. Philadelphia.
- WENZ, W., 1940, Gastropoda, Teil 1, Allgemeiner Teil/Prosobranchia, In: SCHINDEWOLF, O. H., *Handbuch der Paläozoologie*, 6, Lief. 4, p. 721–960. Borntraeger, Berlin.
- WILSON, B. & GILLETT, K., 1971, *Australian Shells*, 168 p., 106 pl. Rutland, Vermont.
- WILSON, B. & GILLETT, K., 1979, *A Field Guide to Australian Shells. Prosobranch Gastropods*, 287 p., 66 pl. Sydney.
- WOODRING, W. P., 1959, Geology and Paleontology of Canal Zone and Adjoining Parts of Panama. Descriptions of Tertiary Mollusks (Gastropods: Vermetidae to Thaididae). [*United States*] *Geological Survey Professional Paper* 306-B: iii + 239 p., pl. 24–38.
- WOODRING, W. & STENZEL, W., 1959, In: WOODRING, W. P., 1959 (as above).
- WRIGLEY, A., 1940, The English Eocene Campanile. *Proceedings of the Malacological Society of London*, 24: 97–112.